

# Three new species of *Sollasella* (Porifera: Demospongiae: Axinellida: Raspailiidae) from Western Australia

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**ABSTRACT** – The sponge genus *Sollasella* has three named species, two from eastern Australia, (Queensland and New South Wales) and one from the western Arabian Sea. Using a combination of morphological and molecular data, we describe three new species from northern Western Australia. We sequenced Cytochrome Oxidase I and two different fragments of 28S to reconstruct genealogical relationships among species in the genus. *Sollasella suttonorum* sp. nov. is closest morphologically to the two previously known Australian species: *S. digitata* Lendenfeld, 1888 and *S. moretonensis* van Soest, Hooper, Beglinger and Erpenbeck 2006. However, *S. ananas* sp. nov., and *S. maraca* sp. nov. show a novel clubbed or oval (rather than digitate or lobed) morphology. These two species contain a unique spicule type (anatriaene-like) not previously reported in the Axinellida. As a consequence of this study the species diversity of *Sollasella* is doubled to six species, with all species confined to the Indian and Pacific oceans.

**KEYWORDS:** morphology, taxonomy, systematics, molecular phylogenetics, sponge

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## INTRODUCTION

The genus *Sollasella* was first established by Lendenfeld (1888). He named *S. digitata*, from New South Wales, as the type species for the genus. Subsequently Hallmann (1914) redescribed the species, providing additional details and images of the lectotype from the NHMUK. Van Soest et al. (2006) determined that *Raspailopsis cervicornis* Burton, 1959 was a second species of *Sollasella* and redescribed that species from type material (NHMUK) as well as freshly collected material from the vicinity of Oman, the type locality. They also described a third species, *S. moretonensis* van Soest, Hooper, Beglinger and Erpenbeck, 2006 from Queensland and Western Australia.

At a higher systematic level, the familial and ordinal placement of the genus was resolved when Sollasellidae Lendenfeld, 1887 was synonymised with Raspailiidae Nardo, 1833 (order Poecilosclerida; van Soest et al. 2006). A more recent study provided molecular evidence which confirmed this systematic placement (Erpenbeck et al. 2007). Consequently, three species of *Sollasella* are currently recognised; there is the type species *S. digitata* Lendenfeld, 1888 from New South

Wales, *S. moretonensis* van Soest, Hooper, Beglinger and Erpenbeck, 2006 from Queensland and Western Australia, and *S. cervicornis* Burton, 1959 from the western Arabian Sea (van Soest et al. 2021). The genus is therefore only known from the Indian and western Pacific oceans.

In this study we describe three new species from the eastern Indian Ocean, Western Australia. We review the morphological characters used to describe species, highlight the importance of some of these, provide additional data and comparisons between species, and a species key. We report the first finding of an anatriaene-like spicule in the Axinellida and discuss the implications of this.

## MATERIAL AND METHODS

Collections of fresh material were made by SCUBA diving, or by trawl or epibenthic sled beyond diving depths, from several localities along the northern Western Australian coast. Specimens were preserved in 70–100% ethanol. Type specimens and slides of *Sollasella digitata* and *S. moretonensis* were

borrowed from the Australian and Queensland Museums respectively. A map shows the location of specimens utilised in this study (Figure 1), with sequenced specimens in Table 1.

For freshly-collected material, subsamples were cut at right angles to the surface and processed using a graded ethanol dehydration and histolene clearing procedure. They were then embedded in paraffin, sectioned at right angles to the sponge surface with a Leitz slide microtome, and mounted on glass slides with EZ-mountant to determine the skeletal arrangement. Spicule preparations were made with nitric acid, washed in distilled water, mounted on glass slides and examined with an Olympus BX50 microscope. For SEM (TM 3030Plus), dissociated spicules were dried, mounted on stubs and sputter coated with gold. For each spicule type, 20 spicules were measured per specimen, except when noted otherwise. Spicule measurements are expressed as min–av–max spicule length / min–av–max spicule width in micrometers. In the three new species descriptions an overall min–av–max spicule length / min–av–max spicule width in micrometers is calculated from the holotype measurements and three paratypes for each species.

Subsamples of tissue were also used to extract genomic DNA, using the DNeasy blood and tissue kit (Qiagen) according to the manufacturer's instructions. Extractions were used in PCR reactions, using primers and conditions outlined in Table 2. All reactions were tried with 1ul of neat extraction first, followed by concentration and dilution series (1:20 and 1:50 were

often successful). PCR amplicons were outsourced for enzymatic clean-up and sequencing via a capillary sequencer (ABI) at the Australian Genome Research Facility, Perth. Raw sequences were assembled, edited and quality checked in Geneious Prime 2020.2.5. They were then aligned using the MAAFT plug in (Kato and Standley 2013) and analysed using PopART (Leigh et al. 2015, TCS algorithm Clement et al. 2002) and IQ-tree (Nguyen et al. 2015, Chernomor et al. 2016, Kalyaanamoorthy et al. 2017). The maximum likelihood phylogeny was midpoint rooted and nodes assessed with 1000 ultrafast replicates. The two fragments of COI were assembled as one continuous piece for haplotype networks, but the 28S fragments do not overlap and were analysed separately. Of the nine specimens with existing data for 28SD3D5 (*S. cervicornis*, *S. moretonensis*, *S. suttonorum*), we re-sequenced six to ensure veracity.

The following acronyms have been used in this paper:

AMS	Australian Museum (Sydney, New South Wales).
NHMUK	Natural History Museum (London, United Kingdom).
NTM	Museum and Art Gallery of the Northern Territory (Darwin, Northern Territory).
QM	Queensland Museum (Brisbane, Queensland).
WAM	Western Australian Museum (Perth, Western Australia).
ZMA	Zoological Museum (University of Amsterdam, Netherlands).

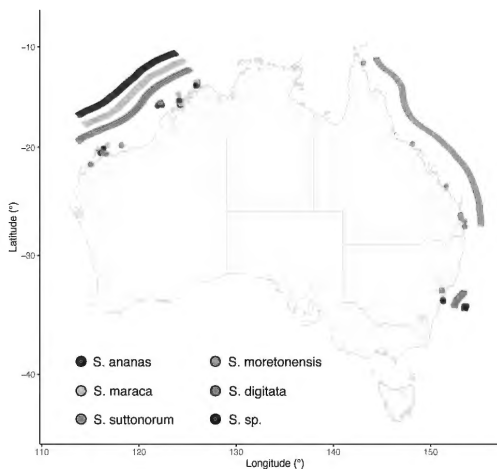


FIGURE 1 Map showing the location of *Sollasella* specimens utilised in this study, excluding *S. cervicornis*, Oman. Dots represent specimens and offset lines represent species distributions.

## RESULTS

The haplotype networks showed varying levels of resolution. The COI network (Figure 2) differentiates among all species except *S. ananas* and *S. maracaca*, as well as recovering two haplotypes within *S. suttonorum*. The 28S D3–D5 fragment recovers a single haplotype network for all included species and shows 6 mutational steps between *S. ananas* and *S. maracaca*. The 28S C-region fragment shows the most resolution and recovers a single haplotype network for all included species as well as 24 mutational steps between *S. ananas* and *S. maracaca*.

The concatenated maximum likelihood phylogeny (Supplementary Figure 1) shows two main lineages. One contained the two new species with club-like or oval morphology, and the other lineage contained the rest of the species in *Sollasella*. The single specimen of *Sollasella* sp. from NSW (represented only by a single gene) was nested inside *S. suttonorum*, but with a relatively long branch. All other species formed monophyletic clades, although *S. moretonensis* was not highly supported (BS 56). All other species were better supported where testable (*S. ananas* BS 100, *S. maracaca* BS 99, *S. suttonorum* BS 81).

TABLE 1 *Sollasella* specimens sequenced in this study. Holotypes in bold. Depths estimated to nearest metre.

Reg. No.	Species	Location	Depth (m)	Latitude	Longitude	Date	COI	28SD3D5	28S-C
WAMZ88025	<i>ananas</i>	Camden Sound, WA	39	-15.376306	124.139547	21 Mar 2015	MZ408260	MZ409557	MZ409584
WAMZ88421	<i>ananas</i>	Camden Sound, WA	41	-15.725853	124.166978	23 Mar 2015	MZ408261	MZ409559	MZ409585
<b>WAMZ88431</b>	<i>ananas</i>	Camden Sound, WA	16	-15.823992	124.248742	24 Mar 2015	MZ408262	MZ409556	MZ409586
WAMZ90694	<i>ananas</i>	Lynher Bank, WA	72	-15.5608	122.234233	29 Oct 2016	MZ408263	MZ409558	MZ409587
WAMZ95018	<i>ananas</i>	Eclipse Islands, WA	42	-13.870788	125.849004	8 Mar 2016	MZ408264	MZ409555	MZ409588
ZMAPOR17450	<i>cervicornis</i>	Dhofar, Oman	17	16.950433	54.818483	11 Dec 2002	MZ408265	MZ409535	MZ409568
WAMZ87345	<i>maraca</i>	Camden Sound, WA	53	-15.376689	124.248319	15 Mar 2015	MZ408266	MZ409550	MZ409576
WAMZ87779	<i>maraca</i>	Camden Sound, WA	45	-15.253592	124.203039	19 Mar 2015	MZ408267	MZ409554	MZ409578
NTMZ007749	<i>maraca</i>	Camden Sound, WA	36	-15.431364	124.059194	20 Mar 2015	MZ408268	MZ409553	MZ409583
WAMZ87955	<i>maraca</i>	Camden Sound, WA	62	-15.446442	124.083022	20 Mar 2015	MZ408269	MZ409552	MZ409579
WAMZ88085	<i>maraca</i>	Camden Sound, WA	28	-15.711306	124.315778	22 Mar 2015	MZ40827	MZ409549	MZ409581
<b>WAMZ94066</b>	<i>maraca</i>	Maret Islands, WA	33	-14.7208	124.039667	5 Dec 2015	MZ408271	MZ409551	MZ409577
WAMZ95073	<i>maraca</i>	Eclipse Islands, WA	23	-13.536462	125.846464	10 Mar 2016	MZ408272	MZ409548	MZ409580
WAMZ95323	<i>maraca</i>	Eclipse Islands, WA	27	-13.521582	125.906131	14 Mar 2016	MZ408273	MZ409547	MZ409582
QMG303059	<i>moretonensis</i>	Cape Grenville, QLD	31	-11.617	143.069	26 Mar 1993	MZ408274	MZ409536	MZ409567
QMG303205	<i>moretonensis</i>	N Stradbroke Is, QLD	25	-27.418	153.551	2 Jun 1993	-	MZ409538	-
<b>QMG303227</b>	<i>moretonensis</i>	N Stradbroke Is, QLD	30	-27.401	153.533	4 Jun 1993	-	MZ409534	MZ409566
QMG303996	<i>moretonensis</i>	Mooloolaba, QLD	11	-26.602	153.103	9 Feb 1994	-	MZ409537	MZ409562
QMG315719	<i>moretonensis</i>	Noosa, QLD	18	-26.376	153.126	12 Oct 1999	-	MZ409529	MZ409560
QMG315759	<i>moretonensis</i>	Noosa, QLD	21	-26.346	153.067	13 Oct 1999	-	MZ409530	MZ409561
QMG321402	<i>moretonensis</i>	Mooloolaba, QLD	13	-26.645	153.161	18 Aug 2004	-	MZ409531	MZ409563
QMG321796	<i>moretonensis</i>	Gladstone, QLD	10	-23.677	151.618	11 Nov 2004	-	MZ409533	MZ409564
QMG329277	<i>moretonensis</i>	Ayr, QLD	45	-19.625	148.135	28 Nov 2005	MZ408277	MZ409532	MZ409565

Reg. No.	Species	Location	Depth (m)	Latitude	Longitude	Date	COI	28SD3D5	28S-C
AMSZ5725	<i>Sollasella</i> sp.	Malabar, NSW	7	-33.967	151.267	20 Jul 1972	MZ408275	-	-
QMG306153	<i>suttonorum</i>	Port Hedland, WA	37	-19.767	118.217	5 Sep 1995	-	MZ409539	MZ409569
WAMZ05487	<i>suttonorum</i>	Dampier Archipelago, WA	18	-20.585833	116.593833	2 Sep 1999	-	MZ409542	MZ409570
WAMZ65274	<i>suttonorum</i>	Onslow, WA	12	-21.596111	115.060556	26 Mar 2013	MZ408276	MZ409546	MZ409572
WAMZ81703	<i>suttonorum</i>	Pilbara Shelf, WA	37	-20.474722	116.307222	25 Jun 2013	-	MZ409544	MZ409573
<b>WAMZ88378</b>	<i>suttonorum</i>	Onslow, WA	10	-21.620278	115.011944	10 Jul 2015	-	MZ409543	MZ409574
WAMZ94761	<i>suttonorum</i>	Eclipse Islands, WA	25	-13.898364	126.039685	6 Mar 2016	MZ408278	MZ409541	MZ409571
NTMZ007747	<i>suttonorum</i>	Eclipse Islands, WA	27	-13.508897	126.078492	3 Mar 2016	MZ408280	MZ409545	-
WAMZ95470	<i>suttonorum</i>	Lynher Bank, WA	76	-15.6005	122.141033	29 Oct 2016	MZ408279	MZ409540	MZ409575

TABLE 2 Primers and PCR cycling conditions used in this study.

Primer name	Primer sequence	Program	Reference
<b>COI</b>			
SpongeCOI-F1 / dgHCO2198	5'-AGATAGGDACWGCNTTTA-3'/ 5'-TAAACTTCAGGGTGACCAAARAAYCA-3'	94°C 3 mi (94°C 30s, 41°C 30s, 72°C 60s) x35, 72°C 5 mi	Vargas et al. 2015 Meyer et al. 2005
<b>COI</b>			
SpongeCOI-F1 / jg.LCO1490.v2	5'-AGATAGGDACWGCNTTTA-3'/ 5'-TTTCLACIAAYCAYAAARGAYATTGG-3'	94°C 3 mi, (94°C 30s, 50°C 30s, 72°C 45s) x8, (94°C 30s, 48°C 30s, 72°C 45s) x35, 72°C 5 mi	Vargas et al. 2015 Geller et al. 2013
<b>COI</b>			
COX1-D2 / COX1-R1	5'-AAFACTGCTTTTTTIGATCCTGCCGG-3'/ 5'-TGTTGRGGGAAAAARGTTAAAT-3'	95°C 2 mi, 50°C 60s, 72°C 2 mi, (95°C 50s, 48°C 50s, 72°C 2 mi) x35, 72°C 10 mi	Rot et al. 2006 Rot et al. 2006
<b>28s D3-D5</b>			
Por28S-830F / Por28S-1520R	5'-CATCCGACCCGCTTGAA-3'/ 5'-GCTAGTTGATTCGGCAGGTG-3'	94°C 5 mi (94°C 30s, 55-50°C (TD) 30s, 72°C 30s) x10, (94°C 30s, 53°C 30s, 72°C 30s) x25, 72°C 5 mi	Morrow et al. 2012 Morrow et al. 2012
<b>28s C-region</b>			
28S C2 / 28S D2	5'-GAAAAGAAGACTTTGRARAGAGAGT-3'/ 5'-TCCGTGTTTCAAGACGGG-3'	95°C 4 mi, 51°C 2mi, 72°C 2 mi, (95°C 60s, 51°C 60s, 72°C 60s) x35, 72°C 5 mi	Chombard et al. 1998 Chombard et al. 1998

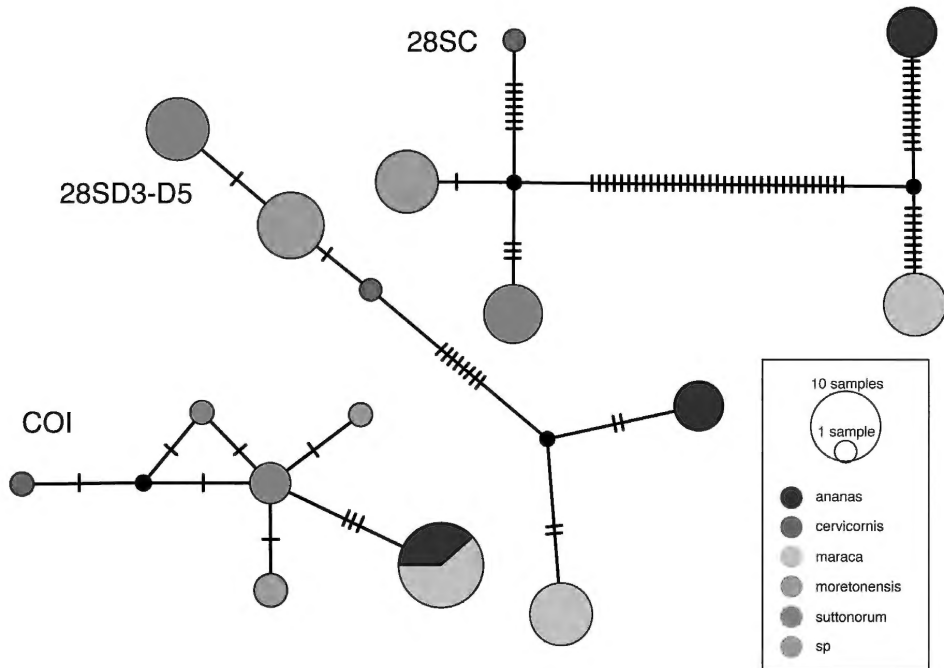


FIGURE 2 Statistical parsimony haplotype network of three gene regions (COI, 28SD3D5, 28S C-region) for species of *Sollasella*. Black circles represent extinct or unsampled haplotypes, hash marks represent one mutational step.

## SYSTEMATICS

### Class Demospongiae Bergquist, 1978

#### Order Axinellida Dendy, 1905

#### Family Raspailiidae Nardo, 1833

#### Genus *Sollasella* Lendenfeld, 1888

#### DEFINITION

Emended from van Soest et al. 2006: Raspailiidae with a strong axial column of confusedly aligned oxeas and styles/anisostrongyles with extra-axial columns of short oxeas and long and short styles/anisostrongyles positioned at right angles to the axial column. Branching, vasiform or oval morphology typically with a basal stalk, characterised by polygonal to rectangular surface plates surrounded by pores. Oxeas form a continuous cortical palisade of brushes centrally pierced by long styles/anisostrongyles. A low proportion of short acanthostyles may be present. Anatriaene-like spicules occur in two species.

#### TYPE SPECIES

*Sollasella digitata* Lendenfeld, 1888 (by monotypy).

#### *Sollasella suttonorum* Fromont and Wilson, sp. nov.

#### Suttons' sponge

(Figures 1–2, 3–8, 15; Tables 3–4)

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#### DEFINITION

Branching *Sollasella* that are dichotomous, rounded apically, stalked basally, with small pores defining the edges of surface polygonal plates. Surface hispid in parts, usually apically or intermittently on the sides of branches. Firm and compressible texture. Spicules are smooth oxeas with a large size range and very large anisostrongyles. Skeleton divided into three parts: axially condensed central core, subcortical region of lower spicule density with spicule brushes crossing from the core to the cortex, and a surface cortical region.

#### MATERIAL EXAMINED

##### *Holotype*

**Australia: Western Australia:** Wheatstone, Onslow, Pilbara, 21°37'13"S, 115°00'43"E, 9 m depth, 10 July 2015, J. Fromont, M.A. Wahab, stn. RVS6222/D11-T4, SCUBA, WAMSI Onslow Survey II July 2015 (WAM Z88378<sup>DNA</sup>).

### Paratypes

**Australia: Western Australia:** Enderby Island, Dampier Archipelago, Pilbara, 20°35.15'S, 116°35.63'E, 17 m depth, 2 September 1999, J. Fromont, stn. DA3/99/55, SCUBA, Woodside Dampier Expedition III 1999 (WAM Z5487<sup>DNA</sup>); Bare Rock, Pilbara, 20°28'29"S, 116°18'26"E, 36–38 m depth, 25 June 2013, E. Morello, G. Fry, M. Miller, D. Thomson, D. Bearham, stn. PMCP/118, sled, CSIRO Pilbara Seabed Biodiversity Characterisation & Mapping survey 2013 (WAM Z81703<sup>DNA</sup>); Eclipse Islands, Kimberley, 13°53'54.110"S, 126°02'22.867"E, 24 m depth, 6 March 2016, O.A. Gomez, J.A. Ritchie, stn. SOL79/WA079, epibenthic sled, WAMSI Survey 3 Eclipse Islands March 2016 (WAM Z94761<sup>DNA</sup>); Lynher Bank, Kimberley, 15°36'01.800"S, 122°08'27.720"E, 76 m depth, 29 October 2016, J. Fromont, J.A. Ritchie, stn. SOL20/WA110, epibenthic sled, WAMSI Survey 4 Lynher Bank Oct–Nov 2016 (WAM Z95470<sup>DNA</sup>); Eclipse Islands, Kimberley, 13°30'32.030"S, 126°04'42.572"E, 26–27 m depth, 3 March 2016, O.A. Gomez, J.A. Ritchie, stn. ECL45/WA072, epibenthic sled, WAMSI Survey 3 Eclipse Islands March 2016 (NTM Z007747<sup>DNA</sup>).

### Other material

**Australia: Western Australia:** SW of Cape Jaubert, -19.7666666666667, 118.216666666667, 37 m depth, 5 September 1995, S. Cook, RV Southern Surveyor, by trawl (QM G306153<sup>DNA</sup>); Wheatstone, Onslow, Pilbara, 21°35'46"S, 115°03'38"E, 12 m depth, 26 March 2013, J. Fromont, E. Buettner, stn. RVS5737/D10-T4, SCUBA, WAMSI Onslow Survey I March 2013 (WAM Z65274<sup>DNA</sup>).

### Material examined for comparison

**Australia: New South Wales:** *paralectotype* *Sollasella digitata*, Port Jackson, Sydney, 33°51'S, 151°16'E (AMS G9107); *Sollasella* sp. east of Malabar, Sydney, 33°58'S, 151°16'E, 7 m depth, 20 July 1972, Australian Museum Shelf Benthic Survey (AMS Z5725<sup>DNA</sup>). **Queensland:** holotype, *Sollasella moretonensis*, Middle Reef, N of North Stradbroke Island, 27.40083°S, 153.53°E, 30 m depth, 4 June 1993, J.N.A. Hooper, J.A. Kennedy, SCUBA (QM G303227<sup>DNA</sup>); *paratype* (QM G321402<sup>DNA</sup>) and 7 other specimens (QM G303996<sup>DNA</sup>, QM G331599<sup>DNA</sup>, QM G315649<sup>DNA</sup>, QM G315759<sup>DNA</sup>, QM G303205<sup>DNA</sup>, QM G315759<sup>DNA</sup>, QM G303059<sup>DNA</sup>; collection details in van Soest et al. 2006).

### DESCRIPTION

Stalked branching sponge. Branches rounded apically, frequently dichotomous (Figure 3). Distinctive polygonal plates (largest 3 x 3 mm) over surface, with numerous small pores (0.05 mm) outlining polygon edges. Surface hispid apically and intermittently along sides of branches from spicules extending to 3 mm; stalk and most of branch surfaces not hispid (Figure 4). Consistency firm and compressible (preserved 75% ethanol), or incompressible (100% ethanol).

**Dimensions:** holotype WAM Z88378 overall height x width x breadth 110 x 75 x 15 mm, stalk height x width x breadth 40 x 25 x 15 mm, branches height x width x breadth 70 x 15 x 13 mm; largest specimen WAM Z95470 overall height x width x breadth 140 x 90 x 17 mm, stalk height x width x breadth 50 x 17 x 15 mm, branches height x width x breadth 90 x 15 x 13 mm. Color *in vivo* reddish brown, in ethanol dull grey, or brown if covered in sediment.

**Skeleton:** The sponge body is clearly divided into three parts (Figure 5). Oxeas, anisostrongyles and fibre arranged longitudinally, form a dense axial region up to 5 mm wide. At right angles to the surface, oxeas form dense brushes with a central anisostrongyle, forming a cortical region 1 mm wide (Figure 6). Anisostrongyles extend beyond the surface to 3 mm. In between is a subcortical region of lower spicule density, 3 mm wide, with spicule brushes crossing from the core to the surface cortex. Brushes taper from the cortex to the axial core. The skeletal layout is the same in the branches and in the basal stem.

**Spicules:** Spicules are abundant oxeas with a large size range, usually straight, occasionally curved, rarely wavy, with long hastate tapering points that are occasionally acerate, rare anisostrongyle forms: size 240–645–1010 x 4–16.2–35 µm (Figure 7, Tables 3–4). Anisostrongyles that are extremely long, straight: size 2500–4609–7200 x 22–44.6–68 µm (Figure 15, Tables 3–4). No acanthostyles.

### ECOLOGY

Collected from 9–38 m depth, on low rocky outcrops or reef, can withstand high sediment load in water column. Barnacle on stalk of WAM Z94761.

### REPRODUCTION

Reproductive elements were not observed.

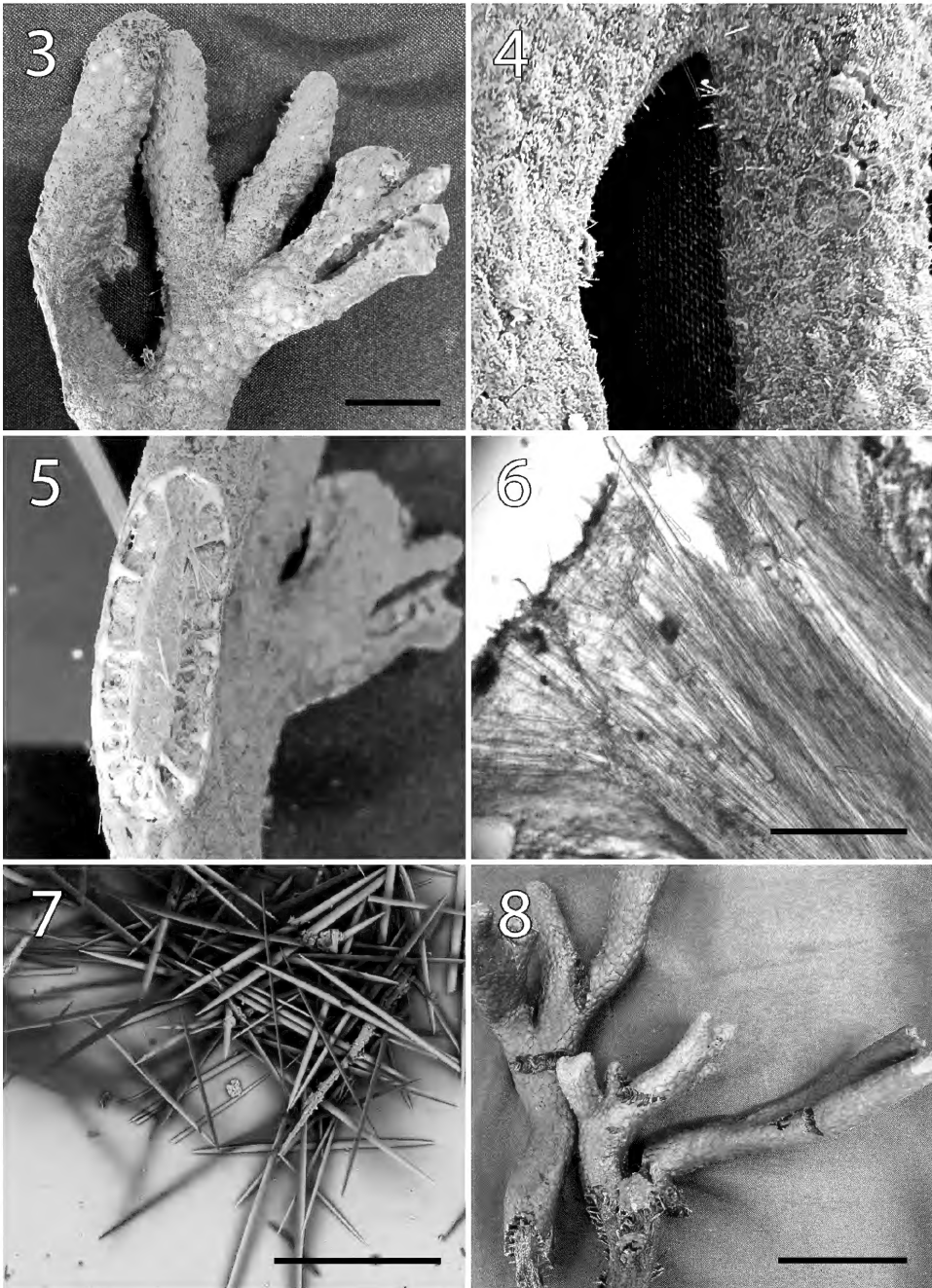
### DISTRIBUTION

*Sollasella suttonorum* sp. nov. is restricted to the tropical Pilbara and Kimberley regions of Western Australia (Figure 1).

### REMARKS

*Sollasella suttonorum* is distinguished from other species of *Sollasella* by its surface polygons and complement and size range of spicules (Tables 3–4). Although all species of *Sollasella* have surface polygons, oxeas and some form of long spicule, it is the combination found in *S. suttonorum* that is unique.

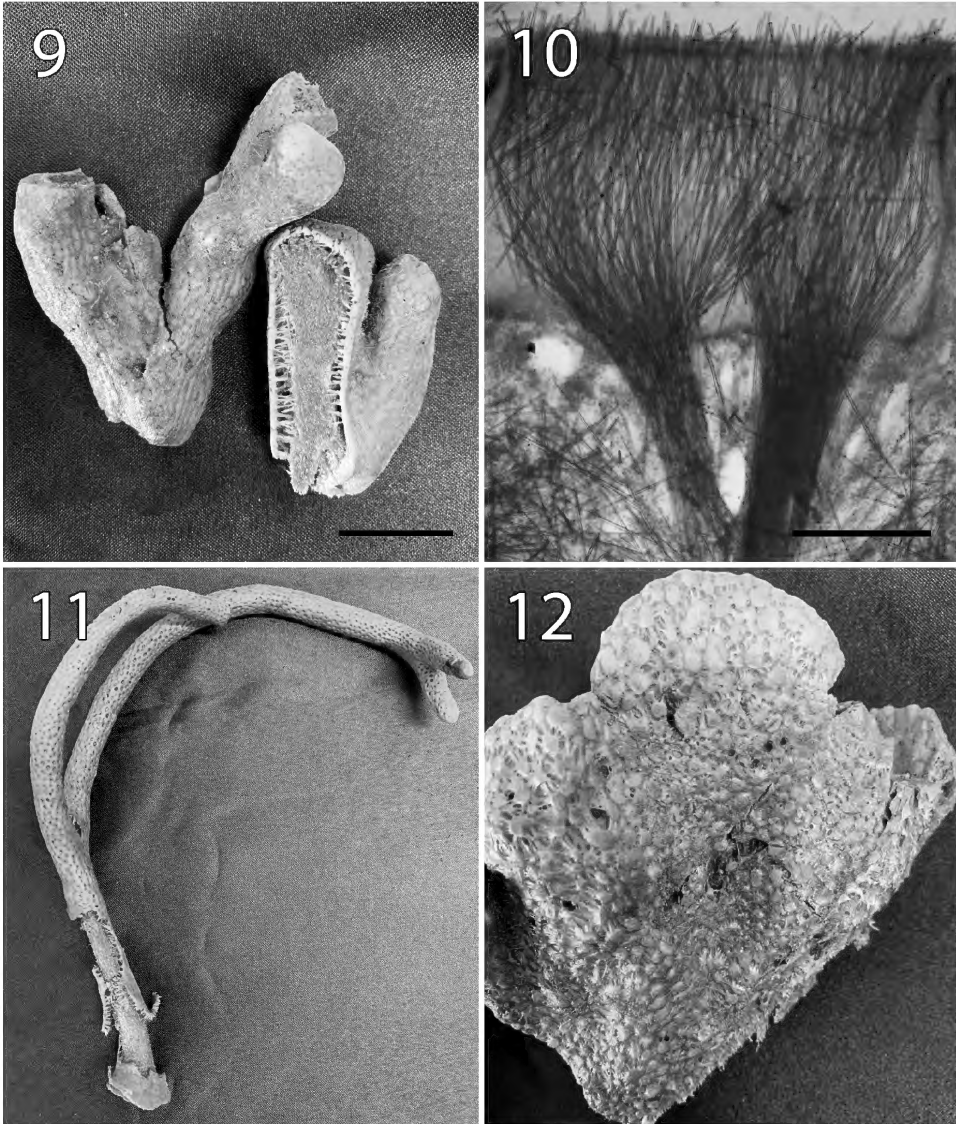
The paralectotype of *S. digitata* (AMS G9107) has oxeas and anisostrongyles (Figure 10) and lacks acanthostyles, as found in *S. suttonorum*. However, the size ranges of the spicules differ with both oxeas and anisostrongyles in *S. digitata* consistently shorter than those in *S. suttonorum* (Table 3, Figures 13, 15). In addition, the surface polygons of *S. digitata* are small



FIGURES 3–8 *Sollasella suttonorum* sp. nov. 3) holotype (WAM Z88378) whole specimen showing rounded apices and polygonal surface plates, scale = 2 cm; 4) paratype (WAM Z95470) close up of surface polygons and hispid sides of branches; 5) holotype (WAM Z88378) longitudinal section through branch showing axially condensed core, subcortical region and cortex; 6) paratype (WAM Z5487) brushes of cortical skeleton showing large central anisostromyngles (broken), scale = 500  $\mu$ m; 7) paratype (WAM Z94761) SEM image of oxeas showing large size range, scale = 500  $\mu$ m; 8) (QM G306153) whole specimen showing branching habit and polygonal surface plates without net-like collagen scale = 2 cm.

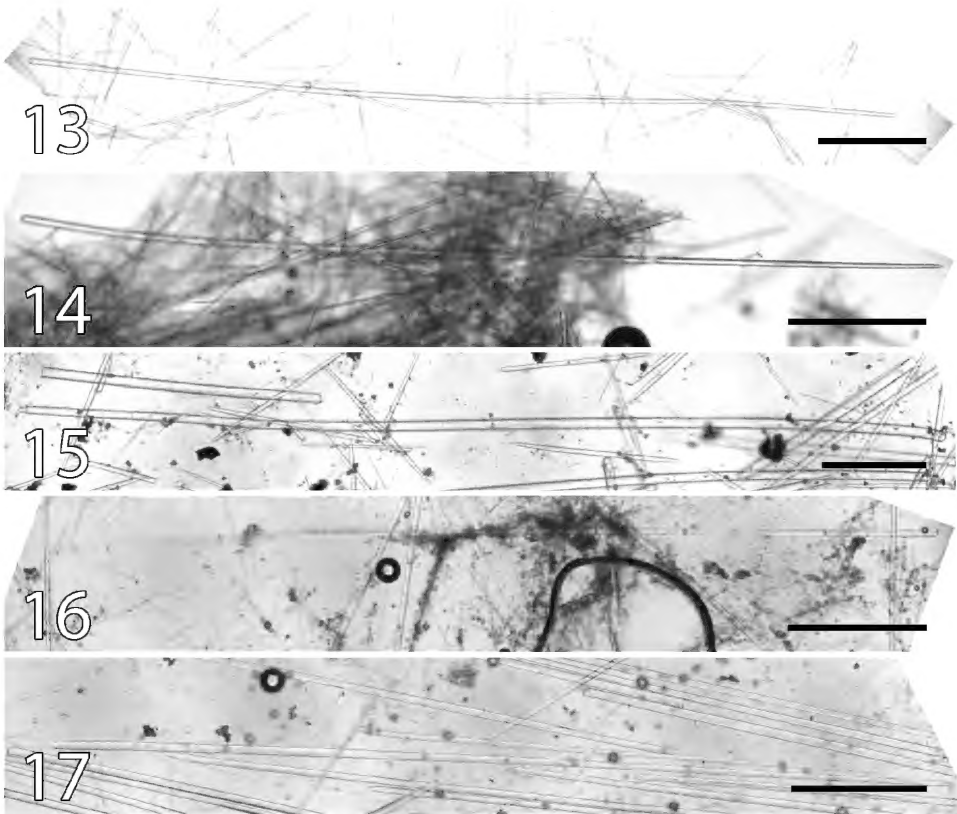
and elongate (Figure 9). Lendenfeld (1888) reported them to be 1–2 mm wide, and Hallmann (1914) noted that the surface structures in the type specimen were ‘much elongated in the longitudinal direction of the branches’, also measuring them as only 1–2 mm wide, concurring with Lendenfeld (1888) on their narrow width.

Our examination of the paralectotype also found the surface structures are narrow and elongate (Figure 9), markedly different from the polygons of *S. suttonorum* which are 3 x 3 mm wide. The narrow, more rectangular structures in *S. digitata* were not noted by van Soest et al. (2006) but this may in part be due to



FIGURES 9–12 9) *Sallasella digitata* syntype (AMS G9107) whole specimen showing rounded apices and small rectangular surface plates on branches, scale = 2 cm; 10) *S. digitata* syntype (AMS G9107) skeleton showing characteristic cortical brushes of oxea, scale = 500  $\mu$ m; 11) *Sallasella* sp. (AMS Z5725) whole specimen showing long, apically bifurcated branches and small surface plates; 12) *S. moretonensis* holotype (QM G303227) whole specimen showing fan-shaped habit and large polygonal surface plates with net-like collagen.





FIGURES 13–17 Large anisostrongyles characteristic of *Sollasella* species. 13) *Sollasella digitata* syntype (AM G9107) scale = 500  $\mu$ m; 14) *S. moretonensis* holotype (QM G303227) scale = 500  $\mu$ m; 15) *S. suttonorum* holotype (WAM Z88378) scale = 500  $\mu$ m; 16) *S. ananas* holotype (WAM Z88431) scale = 1 cm; 17) *S. maraca* holotype (WAM Z94066) scale = 1 cm.

a non type specimen, figured in Hallmann (1914) and reproduced in van Soest et al. (2006), that appears to have polygonal structures.

*Sollasella suttonorum* differs from *S. cervicornis* in size of spicules, with *S. suttonorum* having oxeas and anisostrongyles that are longer than those in *S. cervicornis* (Table 3). The latter species also has abundant smooth styles, of a similar size to the oxeas, not seen in *S. suttonorum* or *S. digitata*. *Sollasella cervicornis* has polygons (4 x 2 mm) which are more elongate than those in *S. suttonorum*.

*Sollasella suttonorum* is very different from *S. moretonensis*. The latter species has larger polygons ( $\leq 5 \times 6$  mm), a vasiform, lobate or fan-shaped morphology (Figure 12) and acanthostyles as part of the spicule complement (Table 3). *Sollasella moretonensis* has two size categories of oxeas, with the smaller category restricted to the ectosomal region (van Soest et al. 2006). Combining these two categories

gives a similar size range of oxeas to that found in *S. suttonorum*, but in the latter species, oxeas of different sizes are not restricted to distinct parts of the skeleton.

One specimen (QM G306153, Figure 8), previously referred to *S. moretonensis* (van Soest et al. 2006, Hooper et al. 2008), was found to conform to *S. suttonorum* in branching morphology, surface polygonal detail, spicule complement and sizes as well as DNA, and has been transferred to this species.

In summary, the branching morphology and combination of surface polygon shape, spicule complement and sizes, characterise *S. suttonorum*.

#### ETYMOLOGY

The new species is named for Jane Fromont's family, David, Zollic and Hanna Sutton, in recognition of their constant support during her career as a sponge biologist, museum curator and head of Aquatic Zoology, Western Australian Museum.

***Sollasella ananas***  
**Fromont and Wilson, sp. nov.**

**Pineapple sponge**

(Figures 1–2, 16, 18–23; Tables 3–4)

urn:lsid:zoobank.org:act:4AB8A295-2C8D-4FA7-BFA2-8D0E5E4D7391

DEFINITION

Oval *Sollasella* that are stalked basally with conspicuous surface polygonal plates. Centre of polygons may be raised. Pores around polygons not visible. Firm, slightly compressible texture. Cream alive and preserved. Spicules are smooth oxeas with a large size range and very large anisostrongyles, anatriaene-like spicules occur axially. Skeleton divided into three parts: axially condensed central core, subcortical region of lower spicule density with spicule brushes crossing from the core to the cortex, and a surface cortical region.

MATERIAL EXAMINED

*Holotype*

**Australia: Western Australia:** Camden Sound, Kimberley, 15°49'26.37"S, 124°14'55.47"E, 16 m depth, 24 March 2015, J. Fromont, L. Kirkendale, stn. SOL105/WA037, epibenthic sled, WAMSI Survey 1B Camden Sound March 2015 (WAM Z88431<sup>DNA</sup>).

*Paratypes*

**Australia: Western Australia:** Camden Sound, Kimberley, 15°49'26.37"S, 124°14'55.47"E, 16 m depth, 24 March 2015, J. Fromont, L. Kirkendale, stn. SOL105/WA037, epibenthic sled, WAMSI Survey 1B Camden Sound March 2015 (WAM Z88325); Camden Sound, Kimberley, 15°43'33.07"S, 124°10'01.12"E, 40 m depth, 23 March 2015, J. Fromont, L. Kirkendale, stn. SOL77/WA034, epibenthic sled, WAMSI Survey 1B Camden Sound March 2015 (WAM Z88421<sup>DNA</sup>); Camden Sound, Kimberley, 15°22'34.70"S, 124°08'22.37"E, 39 m depth, 21 March 2015, J. Fromont, L. Kirkendale, stn. SOL160/WA025, epibenthic sled, WAMSI Survey 1B Camden Sound March 2015 (WAM Z88025<sup>DNA</sup>); Eclipse Islands, Kimberley, 13°52'14.837"S, 125°50'56.414"E, 41–42 m depth, 8 March 2016, O.A. Gomez, J.A. Ritchie, stn. ECLE1/WA084, epibenthic sled, WAMSI Survey 3 Eclipse Islands March 2016 (WAM Z95018<sup>DNA</sup>); Lynher Bank, Kimberley, 15°33'38.880"S, 122°14'03.240"E, 72 m depth, 29 October 2016, J. Fromont, J.A. Ritchie, stn. SOL21A/WA111, epibenthic sled, WAMSI Survey 4 Lynher Bank Oct-Nov 2016 (WAM Z90694<sup>DNA</sup>); Lynher Bank, Kimberley, 15°48'14.100"S, 122°22'03.780"E, 45 m depth, 01 November 2016, J. Fromont, J.A. Ritchie, stn. SOL59/WA114, epibenthic sled, WAMSI Survey 4 Lynher Bank Oct-Nov 2016 (WAM Z90856); Lynher Bank, Kimberley, 15°36'01.800"S, 122°08'27.720"E, 76 m depth, 29 October 2016, J.

Fromont, J.A. Ritchie, stn. SOL20/WA110, epibenthic sled, WAMSI Survey 4 Lynher Bank Oct-Nov 2016 (NTM Z007748); off Mclennan Bank, Pilbara, 20°29'46.32"S, 116°1'34.32"E, 38 m depth, 3 November 2017, B. Alvarez, stn. W18/535, epibenthic sled, CSIRO RV INVESTIGATOR 2017\_05 (WAM Z41922).

*Other material*

**Australia: Western Australia:** Lynher Bank, Kimberley, 15°52'29.160"S 121°55'07.380"E, 49–50 m depth, 22 October 2016, J. Fromont, J.A. Ritchie, stn. SOL15/WA098, epibenthic sled, WAMSI Survey 4 Lynher Bank Oct-Nov 2016 (WAM Z95480); Camden Sound, Kimberley, 15°22'34.70"S, 124°08'22.37"E, 39 m depth, 16 March 2015, J. Fromont, L. Kirkendale, stn. SOL100/WA008, epibenthic sled, WAMSI Survey 1B Camden Sound March 2015 (WAM Z88429); off Mclennan Bank, Pilbara, 20°29'49.56"S, 116°1'22.44"E, 32 m depth, 4 November 2017, B. Alvarez, stn. W18/543, McKenna trawl, CSIRO RV INVESTIGATOR 2017\_05 (WAM Z41559); off Kendrew Island, Pilbara, 20°3'52.92"S, 116°20'49.92"E, 56 m depth, 24 October 2017, B. Alvarez, stn. W84/281, epibenthic sled, CSIRO RV INVESTIGATOR 2017\_05 (WAM Z41889).

DESCRIPTION

Oval sponge tapering to short stalk (Figure 18–20). Distinctive polygonal plates (largest 4 x 4 mm) over surface. Centre of polygons may be raised due to central core of anisostrongyles, most visible when the sponge has been preserved in 100% ethanol (Figure 20). Pores around polygons not visible. Consistency firm and slightly compressible (preserved 75% ethanol), or incompressible (100% ethanol). Stalk may be covered in sediment reflecting the habitat of the sponge (Figure 20).

*Dimensions:* holotype WAM Z88431 overall height x width x breadth 30 x 17 x 16 mm, stalk (incomplete) height 6 x 4 x 4 mm, body height 24 mm; largest specimen WAM Z41889 overall height x width x breadth 48 x 27 x 26 mm, stalk height x width x breadth 11 x 13 x 12 mm, body height 36 mm. Color *in vivo* and in ethanol cream, may have a fine cover of sediment.

*Skeleton:* The sponge body is clearly divided into three parts (Figure 19). Oxeas and anisostrongyles, arranged longitudinally with some spongin reinforcement, form a dense axial region up to 3 mm wide. At right angles to the surface, oxeas form dense brushes with a central anisostrongyle, forming a cortical region 1 mm wide (Figure 19). In between is a subcortical region of lower spicule density, 4 mm wide, with spicule brushes crossing from the core to the surface cortex (width of skeletal regions from holotype). Brushes taper from the cortex to the axial core. Anisostrongyles extend beyond the surface to 1 mm in specimens preserved in 100% ethanol. The stalk has three skeletal components

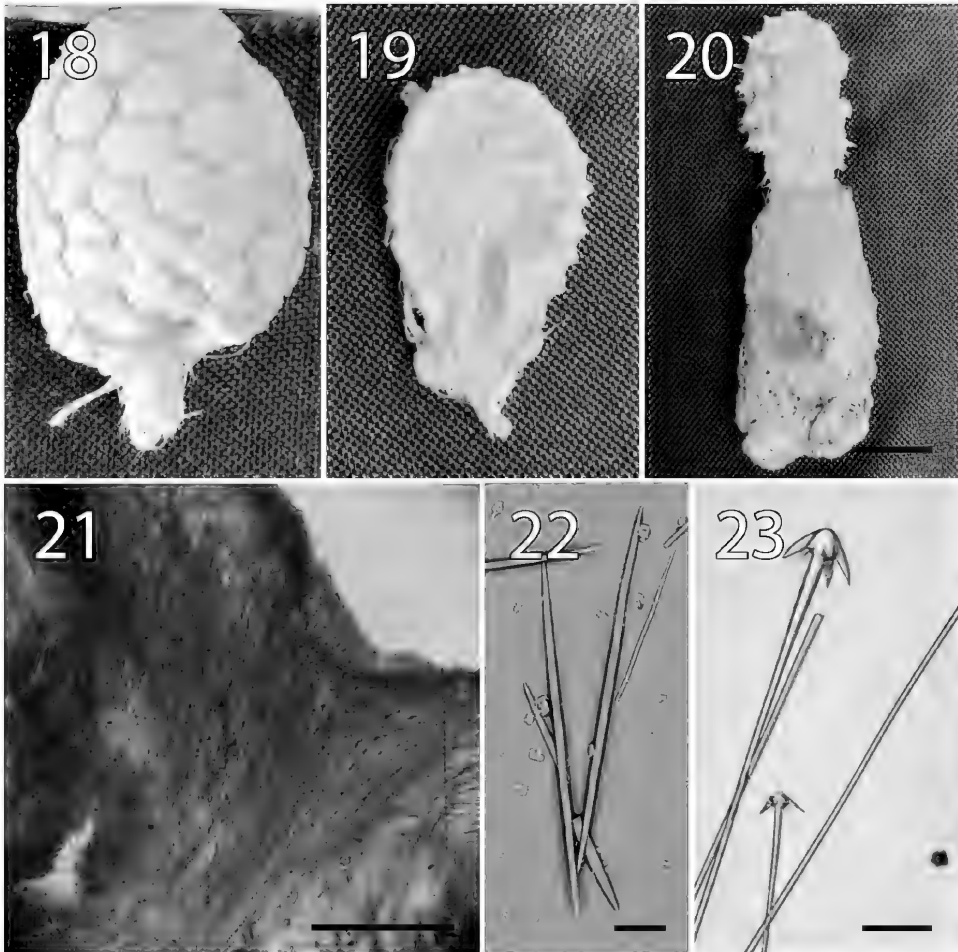
as found in the body of the sponge but with a reduced width in the subcortical region and anatriaene-like spicules axially. The anatriaene-like spicules are most prevalent at the base of the sponge stalk, also occur in the axial skeleton of the stalk and, albeit rarely, in the axis of the sponge body. The clads originate from a central 'tyle' and are recurved (Figure 23).

*Spicules*: Spicules are abundant oxeas with a large size range, usually straight or wavy, long hastate tapering points: size 280–710–990 x 5–11.5–20  $\mu\text{m}$  (Figure 22,

Tables 3–4). Anisostrongyles that are extremely long, straight: size 3920–6303–9250 x 20–39.8–50  $\mu\text{m}$  (Figure 16, Tables 3–4). Anatriaene-like spicules that are extremely long and thin, often sinuous: size 3020–4799–6900 x 2–2.9–4  $\mu\text{m}$  (Figure 23, Tables 3–4). No acanthostyles.

#### ECOLOGY

Collected from 16–76 m depth on low rocky outcrops, which may have cover of sediment.



FIGURES 18–23 *Sollasella ananas* sp. nov. 18) holotype (WAM Z88431) whole specimen showing oval morphology, polygonal plates and short stalk; 19) paratype (WAM Z88421) longitudinal section through whole specimen showing cortex, subcortex and axial core; 20) paratype (WAM Z95018) whole specimen showing anisostrongyles extending from centre of polygons and sediment encrusting basal stalk, scale = 1 cm; 21) holotype (WAM Z88431) skeleton showing characteristic cortical brushes of oxea around long anisostrongyloxeas (broken), scale = 500  $\mu\text{m}$ ; 22) holotype (WAM Z88431) SEM image of oxeas showing long hastate points, scale = 50  $\mu\text{m}$ ; 23) holotype (WAM Z88431) light microscope image of long, thin anatriaene-like spicules, scale = 50  $\mu\text{m}$ .

## REPRODUCTION

WAM Z88431 is a reproductive female containing oocytes, collected in March 2015.

## DISTRIBUTION

*Sollasella ananas* sp. nov. is restricted to the tropical Pilbara and Kimberley regions of Western Australia (Figure 1).

## REMARKS

*Sollasella ananas* is distinguished from all other species of *Sollasella* by its oval external morphology and large polygons such that it resembles a pineapple, and its cream colour. No pores are visible around the polygon edges. The species is most similar to *S. maraca*, which is also oval, but dark brown to black in colour. The size range of oxeas in *S. ananas* is similar to other species of *Sollasella*, but it lacks stylote or strongylote forms. The anisostrongyles are larger than in *S. digitata*, *S. cervicornis*, *S. moretonensis* or *S. suttonorum*, and closest in size to those in *S. maraca* (Table 3). A striking character of this species is the presence of anatriaene-like spicules in the central axis of the sponge; they are most prevalent in the stalk, entwined around the anisostrongyles or forming dense tracts.

## ETYMOLOGY

The name of the new species derives from its external shape and polygonal surface structures which resemble those of a pineapple. 'Ananas' has been adopted by many languages as the name for the pineapple, apparently derived from the Brazilian Tupi word 'nanas'. The name is to be treated as a noun in apposition.

***Sollasella maraca***

**Fromont & Wilson, sp. nov.**

**Maraca sponge**

(Figures 1–2, 17, 24–31; Tables 3–4)

urn:lsid:zoobank.org:act:B4CEF779-D523-4C5C-952C-4EEB98FF8004

## DEFINITION

Elongate oval *Sollasella* that are stalked basally with conspicuous surface polygonal plates. Centre of polygons may be raised. Pores around polygons not visible. Firm, slightly compressible texture. Dark brown to black alive and preserved. Spicules are smooth oxeas, occasionally with strongylote tips, with a large size range, and very large anisostrongyles, anatriaene-like spicules occur axially. Spicules form dense tracts longitudinally in the stalk. Skeleton poorly differentiated into three parts: axial central core, subcortical region with pronounced spicule brushes

crossing from the core to the cortex and a collagenous surface cortical region.

## MATERIAL EXAMINED

*Holotype*

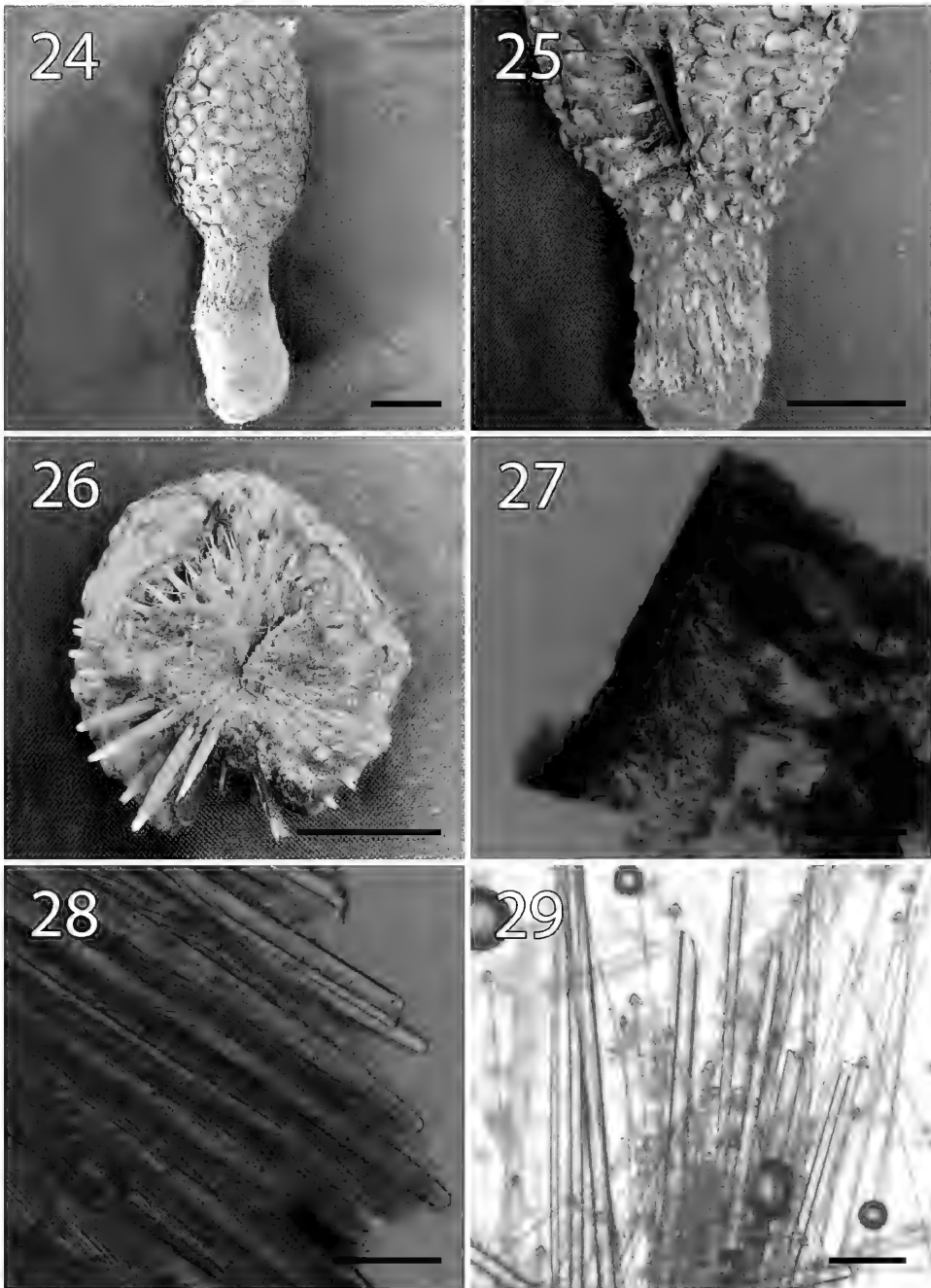
**Australia: Western Australia:** Maret Islands, Kimberley, 14°43.248'S, 125°02.378'E, 32 m depth, 5 December 2015, O.A. Gomez, J.A. Ritchie, stn. SOL52/WA045, epibenthic sled, WAMSIS Survey 2 Maret Islands December 2015 (WAM Z94066<sup>DNA</sup>).

*Paratypes*

**Australia: Western Australia:** Camden Sound, Kimberley, 15°22'36.08"S, 124°14'53.95"E, 52–53 m depth, 15 March 2015, J. Fromont, L. Kirkendale, stn. SOL120/WA005, epibenthic sled, WAMSIS Survey 1B Camden Sound March 2015 (WAM Z87345<sup>DNA</sup>); Camden Sound, Kimberley, 15°25'52.91"S, 124°03'33.10"E, 36 m depth, 20 March 2015, J. Fromont, L. Kirkendale, stn. SOL84/WA021, epibenthic sled, WAMSIS Survey 1B Camden Sound March 2015 (NTM Z007749<sup>DNA</sup>); Camden Sound, Kimberley, 15°42'40.70"S, 124°18'56.80"E, 27–28 m depth, 22 March 2016, J. Fromont, L. Kirkendale, stn. SOL2/WA030, epibenthic sled, WAMSIS Survey 1B Camden Sound March 2015 (WAM Z88085<sup>DNA</sup>); Eclipse Islands, Kimberley, 13°32'11.264"S, 125°50'47.270"E, 21–24 m depth, 10 March 2016, O.A. Gomez, J.A. Ritchie, stn. ECL38/WA087, epibenthic sled, WAMSIS Survey 3 Eclipse Islands March 2016 (WAM Z95073<sup>DNA</sup>); Eclipse Islands, Kimberley, 13°31'17.695"S, 125°54'22.072"E, 27 m depth, 14 March 2016, O.A. Gomez, J.A. Ritchie, stn. ECL40/WA097, epibenthic sled, WAMSIS Survey 3 Eclipse Islands March 2016 (WAM Z95323<sup>DNA</sup>); off Glomar Shoal, Pilbara, 19°44'44.52"S, 116°43'39.72"E, 51 m depth, 21 October 2017, B. Alvarez, stn. W72/198, McKenna trawl, CSIRO RV INVESTIGATOR 2017\_05 (WAM Z41318).

*Other material*

**Australia: Western Australia:** Camden Sound, Kimberley, 15°15'12.93"S, 124°12'10.94"E, 44–45 m depth, 19 March 2015, J. Fromont, L. Kirkendale, stn. SOL32/WA019, epibenthic sled, WAMSIS Survey 1B Camden Sound March 2015 (WAM Z87779<sup>DNA</sup>); Camden Sound, Kimberley, 15°26'47.19"S, 124°04'58.88"E, 61 m depth, 20 March 2015, J. Fromont, L. Kirkendale, SOL4/WA022, epibenthic sled, WAMSIS Survey 1B Camden Sound March 2015 (WAM Z87955<sup>DNA</sup>); Camden Sound, Kimberley, 15°46'58.31"S, 124°22'40.97"E, 33 m depth, 25 March 2015, J. Fromont, L. Kirkendale, stn. SOL97/WA039, epibenthic sled, WAMSIS Survey 1B Camden Sound March 2015 (WAM Z88446); off Violet Island, Pilbara, 20°11'55.32"S, 115°47'21.12"E, 53 m depth, 5 November 2017, B. Alvarez, stn. W49/578, McKenna trawl, CSIRO RV INVESTIGATOR 2017\_05 (WAM Z41580).



FIGURES 24–29 *Sollasella maraca* sp. nov. 24) holotype (WAM Z94066) whole specimen showing oval morphology tapering basally, polygonal plates and pleated appearance of stalk, scale = 2 cm; 25) (WAM Z41318) base of whole specimen and stalk showing thick longitudinal tracts of anisostrongyles in stalk, scale = 2 cm; 26) paratype (WAM Z95073) cross section through whole specimen showing collagenous nature of sponge, lack of differentiation between the three skeletal regions and thick tracts of spicules, scale = 2 cm; 27) holotype (WAM Z94066) cortical brushes densely covered in surface pigment cells, scale = 200  $\mu$ m; 28) holotype (WAM Z94066) skeleton showing end of a thick tract of anisostrongyles, scale = 200  $\mu$ m; 29) paratype (WAM Z95323) light microscope image of long, thin anatriaene-like spicules, scale = 200  $\mu$ m.

## DESCRIPTION

*Dimensions:* holotype WAM Z94066 overall height x width x breadth 110 x 36 x 35 mm, stalk height 45 x 25 x 24 mm, body height 60 mm; largest specimen WAM Z41318 overall height x width x breadth 125 x 56 x 56 mm, stalk height x width x breadth 35 x 24 x 20 mm, body height 90 mm. Color *in vivo* and in ethanol dark brown to black, may have a fine cover of sediment.

*Skeleton:* Elongate oval sponge tapering to stalk (Figure 24–29). Distinctive polygonal plates (largest 5 x 5 mm) over surface. Centre of polygons may have a raised protrusion due to a central core of anisostrongyles (Figure 24). Pores around polygons not visible. Consistency firm and slightly compressible (preserved 75% ethanol), or incompressible (100% ethanol). Relatively long stalk may be covered basally in sediment reflecting the habitat of the sponge (Figure 24). Anisostrongyles form dense tracts longitudinally in the stalk giving a ‘pleated’ appearance (Figure 24–25). Skeleton poorly differentiated into three parts: axial central core, subcortical region with pronounced spicule brushes crossing radially from the core to the cortex (Figures 26–28) and a collagenous surface cortical pigmented region (Figure 27). The stalk has three skeletal components as found in the body of the sponge but with a reduced width in the subcortical region and anatriaene-like spicules axially (Figure 29). The anatriaene-like spicules are most prevalent at the base of the sponge stalk, also occur in the axial skeleton of the stalk and, albeit rarely, in the axis of the sponge body. The clads originate from a central ‘tyle’ and are recurved (Figure 29).

*Spicules:* Spicules are abundant oxeas with a large size range, usually straight or wavy, long hastate tapering points, frequent strongylote modifications, rare stylote: size 270–562–1000 x 4–10.3–18 µm (Figures 30–31, Tables 3–4). Anisostrongyles that are extremely long, straight or slightly curved: size 4250–6589–9600 x 20–55.3–80 µm (Figures 17, 27–28, Tables 3–4). Anatriaene-like spicules that are extremely long and thin, often sinuous: size 4250–6159–6900 x 2–2.9–3 µm (Figure 29, Tables 3–4). No acanthostyles.

## ECOLOGY

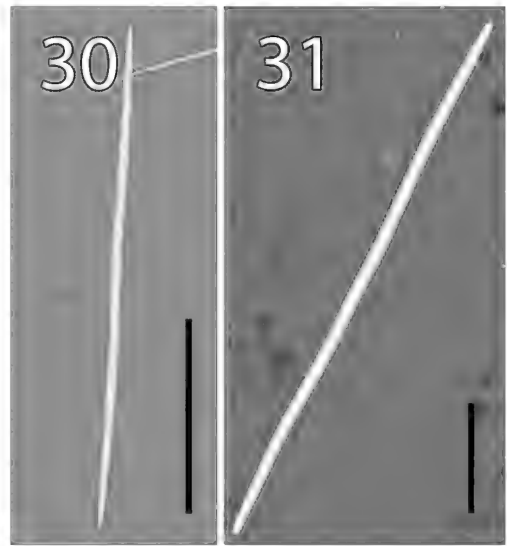
Collected from 24–61 m depth, on low rocky outcrops, which may have cover of sediment.

## REPRODUCTION

Reproductive elements were not observed.

## DISTRIBUTION

*Sollasella maraca* sp. nov. is restricted to the tropical Pilbara and Kimberley regions of Western Australia (Figure 1).



FIGURES 30–31 *Sollasella maraca* sp. nov. 30) holotype (WAM Z94066) SEM image of oxea, scale = 250 µm; 31) holotype (WAM Z94066) SEM image of strongylote form, scale = 100 µm.

## REMARKS

*Sollasella maraca* is distinguished from all other species of *Sollasella* by its elongate oval external morphology, sturdy appearance, long stalk, and large polygons with central protrusions. No pores are visible around the polygon edges. The species is most similar to *S. ananas*, which is also oval, but does not attain the same large size or large stalk as *S. maraca* and is distinctively cream in colour, while *S. maraca* is dark brown to black. *Sollasella maraca* and *S. ananas* have the largest anisostrongyles reported for species of *Sollasella* (Tables 3–4). In addition, *S. maraca* has numerous strongylote modifications of the oxeas, a character not seen in any of the other species of *Sollasella*. Both these species contain anatriaene-like spicules in the central skeletal axis, that are most prevalent in the stalk, entwined around the anisostrongyles or forming dense tracts. This is an extremely unusual spicule for a raspailiid genus and has not been reported before in any Axinellida. The presence of this spicule type is discussed in detail below.

## ETYMOLOGY

The name of the new species derives from its external shape which resembles a maraca. ‘Maraca’ is the Brazilian name for a percussion instrument, and the name is to be treated as a noun in apposition.

**TABLE 3** Spicule measurements of species of *Sollasella*. Measurements are min–av–max length / min–av–max width, in micrometers, and based on holotype measurements for the three new species. Oxea measurements in *S. maraca* are for both oxeate and strongylole forms, \* n=5.

Species	Oxeas I	Oxeas II	Short styles	Subtylostrogyloles/anostrongyloxeas	Acanthostyles	Anatriaene-like spicules*	References
<i>S. digitata</i>	700 x 8	-	-	2000 x 45	-	-	Lendenfeld, 1888
	340 (450–650) 760 x ≤15–16	-	-	2000–≥4000 x 10–35	-	-	Hallmann, 1914
	340–760 x 10–16	-	-	2000–4000 x 10–35	-	-	Van Soest et al., 2006
	430–571–720 x 6–9–10	-	-	2500–3541–4250 x 15–23–30	-	-	present study
<i>S. cervicomis</i>	710–850 x 20–29	-	495–710 x 18–25	1600–3000 x 32–50	-	-	Van Soest et al., 2006
<i>S. moretonensis</i>	660–940 x 14–20	360–515 x 5–8	-	2500–≥4000 x 20–55	95–165 x 3–5	-	Van Soest et al., 2006
<i>S. suttonorum</i>	240–645–1010 x 7–17–28	-	-	2500–4239–5125 x 38–47–50	-	-	present study
<i>S. ananas</i>	280–528–810 x 5–10–15	-	-	3920–5976–7725 x 20–39–50	-	3020–3875–5040 x 3–3.4–4	present study
<i>S. maraca</i>	330–528–730 x 5–9–13	-	-	4545–6094–7300 x 38–50–58	-	4400–5455–6875 x 2.5–3–3	present study
<i>Sollasella</i> sp.	440–641–900 x 12–17–20 (n=8)	-	-	3450–3575–3700 x 50–53–55 (n=3)	-	-	present study

**TABLE 4** Spicule measurements of paratype specimens of the three new species of *Sollasella*. Measurements are min–av–max length / min–av–max width, in micrometers (<sup>1</sup> n=20, <sup>2</sup> n=10, <sup>3</sup> n=5, \* both oxeate and strongylole forms measured and grouped under 'oxeas').

Species	Specimen number	Oxeas <sup>1</sup>	Anisostrongyloxeas <sup>2</sup>	Anatriaene-like spicules <sup>3</sup>
<i>S. suttonorum</i>	WAM Z5487	380–657–960 x 8–12–18	3175–4302–5375 x 22–30–40	-
	WAM Z81703	370–635–910 x 8–13–20	3750–4300–4775 x 22–42–50	-
	WAM Z94761	360–679–1000 x 9–22–35	4600–5595–7200 x 55–60–68	-
<i>S. ananas</i>	WAM Z88421	300–641–970 x 6–11–16	5375–6257–7125 x 30–43–50	4500–5180–6300 x 2–2.6–3
	WAM Z95018	310–654–990 x 8–13–20	5000–6950–9250 x 20–39–50	3700–4730–6900 x 2–2.6–3
	WAM Z41922	380–657–960 x 8–12–18	3920–6029–9250 x 20–38–50	4900–5410–6050 x 3–3–3
	WAM Z87345	370–634–1000 x 4–12–18	4250–6255–9600 x 20–47–70	4250–6165–7500 x 2.5–3–3.5
<i>S. maraca</i> *	WAM Z95073	270–540–790 x 4–10–12	7550–8015–8250 x 60–68–80	5500–5865–6250 x 2.0–2.8–3
	WAM Z95323	320–544–780 x 5–10–12	5000–5990–7225 x 48–56–65	5500–7150–8250 x 2.5–2.9–3

### KEY TO SPECIES OF *SOLLASELLA*

- 1 Branching, lobed or fan-shaped ..... 2  
    Oval-shaped, anatriaene-like spicules present ..... 5
- 2 Lobed or fan-shaped, net-like collagenous surface....  
    .....*S. moretonensis*  
    Branching, no net-like collagenous surface..... 3
- 3 Small, narrow (1–2 mm wide) surface meshes, large  
    anisostrongyles (2000–4000 mm) .....*S. digitata*  
    Polygonal surface meshes, large styles/anisostrongyles  
    (1600–7500 mm) ..... 4
- 4 Abundant smooth styles (495–710 mm), western  
    Arabian Sea .....*S. cervicornis*  
    No smooth styles, eastern Indian Ocean .....  
    .....*S. suttonorum*
- 5 External colour cream..... *S. ananas*  
    External colour dark brown to black ..... *S. maraca*

### DISCUSSION

We report two remarkable findings from this study. The first is the presence of anatriaene-like spicules in *S. ananas* and *S. maraca* (Figures 23, 29) and the second is the novel clubbed or oval (rather than digitate or lobed) morphology found in these species. Initially, we speculated that the novel spicules may not have been found previously in raspailiid species because the base of the stalk had not been present on specimens examined. This was the region where the anatriaene-like spicules were most prevalent in this study. All the specimens of *S. ananas* and *S. maraca* were collected by dredge or sled and the majority of the stalk bases were intact with sediment and substrate adhering to them. Alternatively, many of the branching specimens of *S. suttonorum* and *S. moretonensis* had been collected on SCUBA and did not have the stalk base attached; however, those that did were subsequently examined and did not contain anatriaene-like spicules. Consequently, we note that this spicule type is unique to *S. ananas* and *S. maraca* in the genus *Sollasella*. It would be of merit in future studies to examine other raspailiid genera to see if this spicule type is present.

Anatriaene-like spicules have never been reported from the Raspailiidae or the Axinellida. The spicules are extremely long, thin and fragile and occur next to anisostrongyles in the stalks of *S. ananas* and *S. maraca*. They were particularly prevalent at the base of the sponge and were found in all specimens of both species where the stalks were intact. We carefully examined the sediment at the base of the sponge and the axis of the stalk and found that they were not foreign spicules, sourced from the habitat, but intricately associated with the skeleton of the sponge. We consider

them to be ‘anatriaene-like’ spicules as they may not be homologous to Tetractinellida anatriaenes. Fromont and Bergquist (1990) were the first to suggest that spicules considered to be of the same structural type, e.g. sigmas, may not be homologous. Erpenbeck et al. (2006) noted detailed functional distinctions of characters are required to disprove convergent evolution in what appear to be identical spicule types. More recently, Vacelet and Cárdenas (2018) reported an example of homoplasy, reporting a spicule similar to a euaster, in a genus in the Poecilosclerida. They concluded that the ‘asters’ may be derived from pseudoastrose acanthostyles but with complete loss of the spicule shaft. Much more detailed structural analysis of the anatriaene-like spicules found in this study will be required to determine if they are true anatriaenes but this is beyond the scope of this study. Consequently, we have not revised the diagnosis of Raspailiidae or Axinellida here.

Species of *Sollasella* can be distinguished by external morphological characters, the types of spicules present and details of spicule morphology. Of the six species of *Sollasella* now known, three have an erect branching morphology, with mostly dichotomous branches: *S. digitata*, *S. cervicornis* and *S. suttonorum* sp. nov. Among the branching species, *S. cervicornis* is the only one with relatively common small styles in the same size range as oxeads. All six known species have distinctive surface plates that are usually polygonal but can be rectangular (*S. digitata*). All included species are delimited by molecular data, but it bears repeating that the 28S-C region contains much more information than the traditionally used barcoding fragment of the COI gene (including the suggested addition of the second half of COI), as discussed by Erpenbeck et al. (2016). Here it showed great resolution among species, and we encourage this marker to be used more widely addressing species-level problems in sponges.

*Sollasella moretonensis* is unique within the genus for a number of reasons. This is the only species with a vasiform, lobate or fan-shape. The surface texture of net-like collagenous low ridges between polygons is a synapomorphy for the species. In addition, small acanthostyles are relatively common in this species but have only been rarely reported in *S. cervicornis* and not at all in the four other species. The two new species with oval morphologies, *S. ananas* and *S. maraca*, extend the diagnosis of the genus beyond branching, lobate and fan-shaped morphologies.

The large spicules in this genus have previously been referred to as styles (Lendenfeld 1888; van Soest et al. 2006). However, Hallmann (1914) referred to them as subtylostongyles and his figure 1a<sup>1</sup> depicted one rounded spicule tip being wider than the other. This figure was reprinted in van Soest et al. (2006) and these authors, although calling the spicules styles, noted that Hallmann (1914) referred to them as ‘tylostongyles’. Examination of the paralectotype shows the ‘tyle’ (a rounded swelling on a spicule, Boury Esnault and Rützler 1997) barely exists, and in *S. digitata* this



spicule is more correctly an anisostrongyle, with both ends rounded, albeit unequally. We also found that the holotype of *S. moretonensis* had anisostrongyles, as did the three new species: *S. suttonorum*, *S. ananas* and *S. maraca* (Figures 13–17). We were not able to examine material of *S. cervicornis* but recommend this be done in the future. There was also variation in the oxeas found in these species. *Sollasella cervicornis* is reported to have abundant stylote modifications not seen in any other species (van Soest et al. 2006), while we found common strongylote forms in *S. maraca*, a spicule not reported in any other species. In *S. moretonensis*, *S. ananas* and *S. maraca* the oxeas generally have long hastate tapering points, while *S. suttonorum* had some acerate modifications and *S. digitata* has hastate oxeas and others with acerate or stepped tips. These oxeote modifications may be species specific.

We examined an undetermined specimen collected in New South Wales in 1972 (AMS Z5725) and obtained some sequence data (Folmer fragment of COI). However, we could not compare it genetically to *S. digitata*, as the paralectotype of this species did not amplify for any gene regions (AMS G9107, Erpenbeck et al. 2007), but we did see some morphological similarities that suggest it may be this species. It has small, rectangular surface meshes (Figure 11) currently only seen in *S. digitata* and the oxeas and anisostrongyles were similar in length to this species but thicker (Table 3). However, it has much more elongate branches than the paralectotype of *S. digitata*. The recollection of fresh, sequence-able material of *S. digitata* from near the type locality is necessary to establish the identity of the species, as there is still no genetic information available for the type species of the genus. If furnished, this data could provide information on the genetic distances between the species, and allow testing of the monophyly of the genus, the application of the genus name and its relationship to other raspailiid genera.

The original publication listed the type locality of *S. digitata* as 'east coast of Australia' but subsequent publications also clarified this as Port Jackson and Manly Beach; the AMS original hard copy register has 'E. Australia' for one paralectotype (G.3630 — part from British Museum of Natural History specimen) and Port Jackson (G.9107) for another (Stephen Keable, pers. comm.). The paralectotype G.3630 has a note added in the AMS 'Although recorded as a slide by Hooper and Weidenmayer (1994) material was located as a dry fragment in the non-type collection October 2020 and placed with other dry Porifera type specimens. The form of object as a dry fragment is more consistent with the original hard copy register entry from 1901 which indicates the material was presented by Prof. Arthur Dendy and the top of the page indicates fragments of Lendenfeld's types from the British Museum. Possibly this fragment should be considered Schizotype material'.

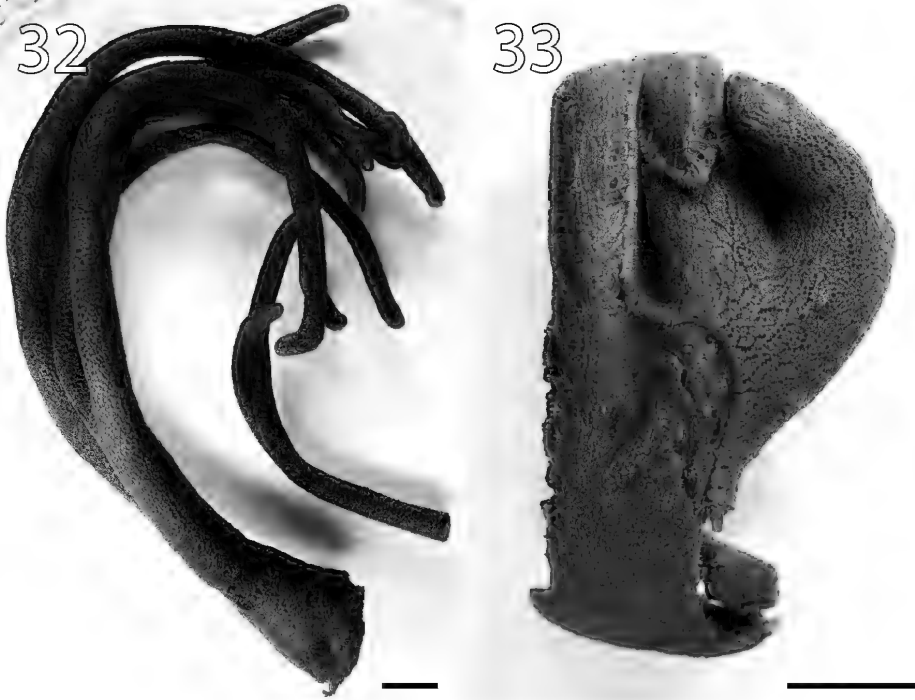
Bergquist identified two other specimens as *S. digitata* that were collected in NSW in the 1970s and are in the AMS collection. Although we have not

physically examined these specimens, images of these (AMS Z15997 and Z4306) indicate they have the small, rectangular surface meshes that are characteristic of this species (Figures 32–33). This is particularly obvious in AMS Z15997 (Figure 32), while in AMS Z4306 (Figure 33) parts of the surface have rectangular surface meshes and others have elongate polygons. These are reminiscent of the figure of *S. digitata* in van Soest et al. (2006) suggesting that surface morphology in *S. digitata* is variable. However, the polygons do not resemble those found on the other four Australian species. It appears that few specimens of *Sollasella* have been collected in NSW, the type specimens in the 1800s and three others in the 1970s, whereas the other Australian species have abundant material.

This study increased the number of *Sollasella* species worldwide from three to six, but this may be an underestimate with sponges in many areas of the world still poorly studied (van Soest et al. 2021). The area of this study was restricted to north Western Australia yet resulted in three new species being discovered. Although the genus is restricted to the Indian and Pacific oceans, the diversity of species is clearly concentrated in the Australian region, with five of the six species recorded there. Furthermore, with the three new species in this publication, the tropical region of Western Australia is the most speciose region globally for the genus. This finding supports earlier reports by Hooper (1991) and Fromont (2003) that northern Western Australia has a disproportionately high number of raspailiid species, with high local endemism. Other sponge genera and families also have high diversity in northern Western Australia e.g. *Ianthella* (Kelly Borges and Bergquist 1995) and *Caulospongia* (Fromont 1998).

As well as being a region of high marine diversity, the north west shelf of Australia is a centre of endemism for many invertebrate groups (Wilson 2013). There is evidence of in situ speciation and radiation of benthic shelf species, especially in genera that lack pelagic larvae (Wilson 2013). This pattern is indicative of a former Tethyan distribution (with the current Indo-West Pacific region the largest remnant of the Sea of Tethys) followed by extinction on the Eurasian shelf (Wilson 2013). In the late Jurassic Period (160 mya) Australia formed part of the supercontinent Gondwana and only the west coast of Western Australia was open to the Tethys Sea, after India had drifted away (Marsh and Fromont 2020). The Australasian continental plate abutted the Indo-West Pacific and consequently the Australian north-western margin became proximal to the world's greatest centre of marine biodiversity (Wilson 2013). Pisera et al. (2017) considered the disjunct distribution of *Vetulina* (Demospongiae: Sphaerocladina: Vetulinidae), with the type species from the Caribbean and the only other two known species reported from northern Western Australia, to be an example of relict faunas that had their origin in the Tethys Sea.

Most species of *Sollasella* have relatively restricted distributions. *Sollasella digitata* is only known from



FIGURES 32–33 *Sollasella digitata*. 32) elongate branching specimen with narrow, elongate surface meshes (AMS G15997), scale = 2 cm; 33) small specimen with small polygonal meshes on some surfaces and irregular elongate meshes on others (AMS Z4306), scale = 2 cm.

New South Wales and has only been collected on three occasions, all in the 1970s, since the type specimens were found. *Sollasella moretonensis* was reported from Queensland and Western Australia, but we found the Western Australian specimen (QM G306153) conformed to *S. suttonorum* in molecular and morphological characters and have transferred the specimen to the new species. This means that *S. moretonensis* only occurs in Queensland. *Sollasella cervicornis* has only been found in the north-western Indian Ocean and *S. suttonorum*, *S. ananas* and *S. maraca* only from northern Western Australia. The characteristic surface plates make this genus distinctive and hopefully the reporting of these three new species will inspire scientists and divers to look for more. Furthermore, the reporting here of an anatriaene-like spicule in a non-tetractinellid genus may prompt research in testing spicule homologies.

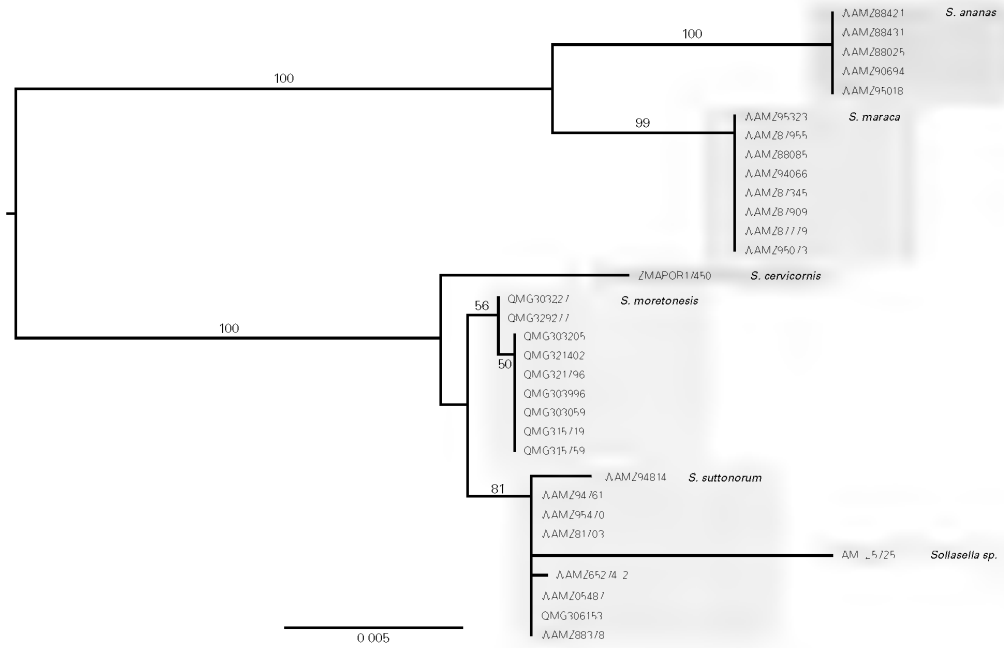
#### ACKNOWLEDGEMENTS

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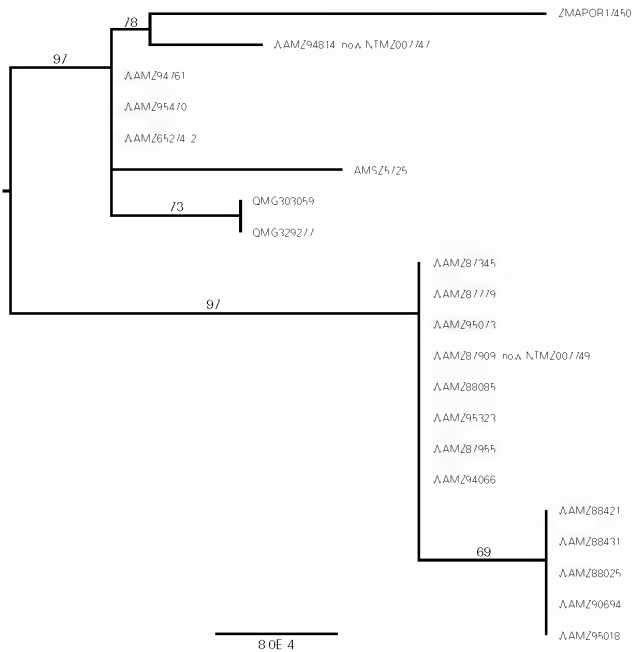
facilitated the loan of specimens from the Australian and Queensland museums respectively and Dr Dirk Erpenbeck kindly provided a fragment of ZMA Por 17450 for sequencing. Michelle Condy, Alex Hickling and Priya Krishnamurthy assisted with sequencing, and Kiah Grogan with making figures. Collections from the Pilbara were funded by the WAM Woodside Dampier project, the Western Australian Marine Science Institute (WAMSI) Dredging Filter Feeders Project 6.3 to WAM and AIMS (Permit Numbers: DEC SF008483, WAFi 2183), the Pilbara Marine Conservation Project (Permit Numbers: DoF 2142 & 2268) and the CSIRO RV Investigator 2017 project (Permit Number: AU-COM2017-378). Kimberley collections were funded by Woodside Energy (Permit Numbers: DoF 2085, 066-RRRW-130723-01) and the Western Australian Marine Science Institute (WAMSI) Kimberley Node Project 1.1.1 to WAM, AIMS and CSIRO (Permit numbers: SF010720, (DoF) 2721). This study was supported by a Gorgon Barrow Island Net Conservation Benefits grant to the Western Australian Museum administered by the Western Australian Department of Parks and Wildlife. The manuscript benefited from the constructive comments of two reviewers.

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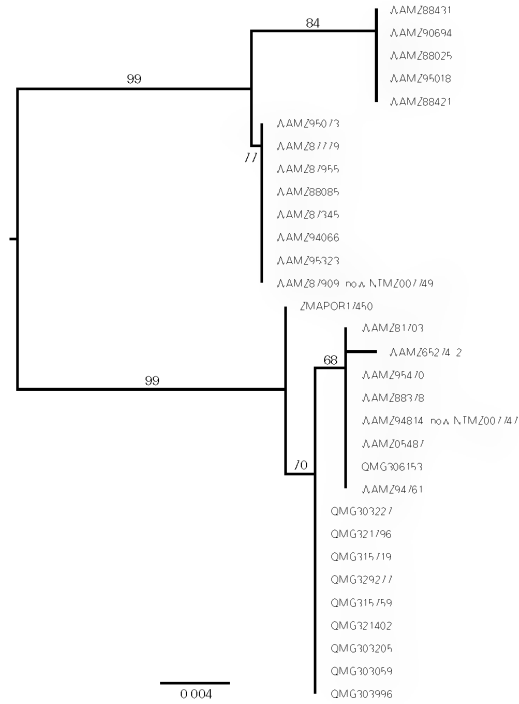
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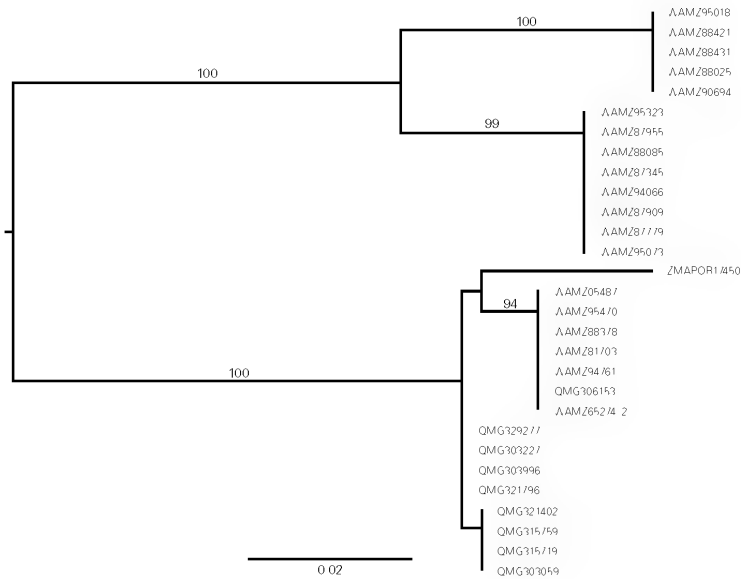
SUPPLEMENTARY FIGURE 1 Maximum likelihood concatenated tree of *Sollasella* specimens (COI, 28S D3D5, 28S C-region) with mid-point rooting.



SUPPLEMENTARY FIGURE 2 Maximum likelihood concatenated tree of *Sollasella* specimens (COI) with mid-point rooting.



SUPPLEMENTARY FIGURE 3 Maximum likelihood concatenated tree of *Sollaseilla* specimens (28S D3D5) with mid-point rooting.



SUPPLEMENTARY FIGURE 4 Maximum likelihood concatenated tree of *Sollaseilla* specimens (28S C-region) with mid-point rooting.

SHORT COMMUNICATION

# Synonymy of two west coast *Lerista* (Reptilia: Scincidae) species

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## INTRODUCTION

The taxonomic descriptions of reptiles of the late Glen M. Storr (1921–1990) are notable for both their abundance and brevity (Smith 1991; Adler 2000; Uetz and Stilianou 2018). In the 1960s, 70s and 80s, Storr was an extremely prolific pioneering reptile taxonomist in an area that would prove to be one of the most speciose reptile regions in the world, Western Australia (e.g. Powney et al. 2011). He described over 200 species and subspecies of reptiles and all of his taxonomic papers were sole author works, with a focus on morphology, colour pattern and geography, and without being informed by genetics. Also notable were the pithy, haiku-like abstracts; for example (the entire abstracts, verbatim): ‘The new species, *L. robusta*, is superficially similar to *L. ips* which is redescribed.’ (Storr 1990a, p. 439) and ‘Four taxa are recognized: *C. virgatus clarus* (Storr), *C. carnabyi* nov., *C. plagiocephalus* (Cocteau) and *C. megasticus* nov.’ (Storr 1976). Although he would typically name as paratypes nearly all of the material he consulted, sometimes numbering in the hundreds for a single taxon, on other occasions he was prepared to name new taxa based on very few specimens if they were distinctive morphologically.

Although almost all of Storr’s species and subspecies are still recognised today, several taxa published late in his career when he was finishing many descriptions for inclusion in forthcoming field guides may be suspect. In this paper, we provide arguments that two species of the scincid genus *Lerista* that were published posthumously in 1991 are referable to sympatric or nearly sympatric species. *Lerista talpina* Storr, 1991 is only known from a single pale individual and *L. maculosa* Storr, 1991 is only known from two specimens. Both species were considered to have been synonymised by Aplin and Smith (2001) in a footnote at the end of a checklist of frogs and reptiles of Western Australia (p. 72), and

this move was followed by many subsequent authors — e.g. Wilson and Swan (2003 and all subsequent editions). However, the paper which Aplin and Smith (2001) cite as ‘Aplin et al. (submitted)’ [n.b. listed as ‘in press’ in the references of Aplin and Smith (2001)] in a footnote was not resubmitted after reviews were returned and never published (MAC, pers. obs.) (the full author list and title are: Aplin, K.P., Adams, M. and Cowan, M.A. Systematics and biogeography of the herpetofauna of the Carnarvon region of Western Australia, submitted to the *Records of the Western Australian Museum*). Since no further comments on their status was provided in the Aplin and Smith (2001) checklist footnotes, the formal synonymy of these two species is best achieved through the presentation of evidence and arguments in support of the synonymy. We repeat and embellish the relevant passages from the Aplin et al. original unpublished manuscript to formally synonymise both taxa here.

## Synonymy of *Lerista talpina* Storr, 1991 with *L. petersoni* Storr, 1976

The holotype of *L. talpina* (WAM R74947) remains the only specimen of this putative taxon (Figure 1). No further specimens have been detected, despite intensive searching at the type locality at Bullara Station by B. Maryan (pers. comm.). Members of the *L. nichollsi* species-group with records from the Western Australian Museum (WAM) from the immediate area comprise *L. uniduo* Storr, 1984a (within 2 km), *L. miopus* Günther, 1867 (within 2 km), *L. onslowiana* Storr, 1984 (38 km to the east) and *L. petersoni* Storr, 1976 (70 km to the south-east). Our examination of the type of *L. talpina* revealed the presence of four supraciliary scales (mentioned in the original description) and a lack of fusion between the prefrontal and second loreal scales. These features exclude referral to either

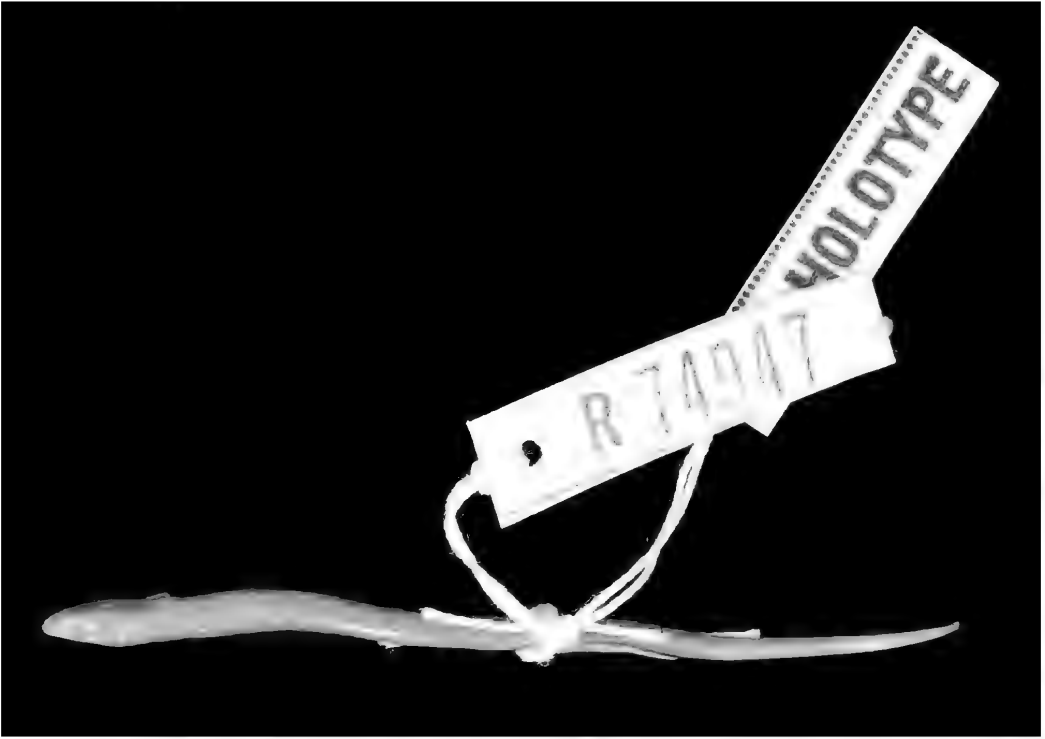


FIGURE 1 Holotype of *Lerista talpina* Storr. Note the lack of any pattern elements, a diagnostic character for this putative species.

*L. uniduo* (three supraciliaries) or *L. onsloviana* (two supraciliaries; prefrontal and second loreal fused) but are consistent with *L. petersoni*. A paravertebral count of 74 is far lower than northern populations of *L. miopus* (usually > 90) but is just below the (as yet poorly defined) range of values for *L. petersoni*. There is a single postsubocular scale on both sides, consistent with *L. petersoni*.

Storr (1984a: 113) initially distinguished WAM R74947 from typical *L. petersoni* on account of its lack of stripes, but later noted its small size, 'small deep-set eyes' and 'lack of ear aperture' (1991a: 145). We have examined the gonads of the holotype and determined that they are very small and macroscopically undifferentiated gonads; thus, the individual is sexually immature. The ear aperture is distinct and strikes us as no more reduced than in many other species of the *L. nichollsi* group, including *L. petersoni*, while the 'deep-set' eyes are most likely attributable to desiccation during preservation (Figure 2). The apparent lack of pattern is intriguing, but by itself is insufficient grounds to maintain this taxon. Accordingly, we relegate *Lerista talpina* Storr, 1991 to a junior synonym of *L. petersoni* Storr, 1976.

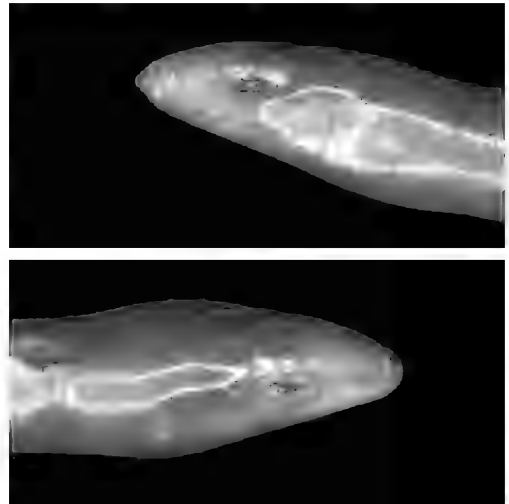


FIGURE 2 Left and right views of the head of the holotype of *Lerista talpina*. Note the appearance of the 'sunken eyes' — presumably a diagnostic character but also potentially from desiccation during the preservation process.

**Synonymy of *Lerista maculosa* Storr, 1991  
with *L. uniduo* Storr, 1984**

*Lerista maculosa* was described from two specimens, the holotype (WAM R95921) from 5 km west of Overlander Roadhouse and a paratype (WAM R92182) from 16 km south of Hamelin Station Homestead. Both localities are on the margin of the Victoria Plateau, but they differ substantially in soil type and vegetation associations.

Storr (1991) distinguished *L. maculosa* from other members of his '*L. nichollsi* complex' only by its heavily spotted pattern (Figure 3). Other members of the *L. nichollsi* species-group with records from the WAM found in sympatry or near *L. maculosa* are *L. uniduo* (in sympatry at both locations), *L. kendricki* Storr, 1991 (in sympatry at Hamelin Station and 30 km south-west of the Overlander Roadhouse site), *L. commivens* Storr, 1972 (in sympatry at both sites), *L. miopus* (in sympatry at Hamelin Station and 17 km south-east of the Overlander Roadhouse site) and *L. praepedita* Boulenger, 1887 (the same occurrence as for *L. miopus*). The holotype and paratype of *L. maculosa* are most like *L. uniduo* in body proportions and in having a 1+2 supraciliary formula and the second loreal fused to the

prefrontal scale. Indeed, apart from having the unusual pattern consisting solely of longitudinal series of spots, they are indistinguishable from sympatric or parapatric *L. uniduo*. In an unpublished PhD thesis, Kendrick (1991: 38) found the paratype to be genetically identical to southern populations of *L. uniduo*, which had been collected within 1 km of the Hamelin locality and also at Overlander Roadhouse (Storr 1984: 116).

In agreement with Kendrick (1991), we consider it most likely that the two specimens of *L. maculosa* are uncommon pattern variants of *L. uniduo*. Other possibilities are that the two *L. maculosa* specimens are products of a rare hybridisation event between *L. uniduo* and another member of this species complex. In either case, we consider it prudent to regard *L. maculosa* as a junior synonym of *L. uniduo*.

**ACKNOWLEDGEMENTS**

We thank G. Shea and D. Chapple for encouraging us to finalise the synonymy from the unpublished Carnarvon Basin survey chapter that was intended to be a companion to McKenzie et al. (2000). We thank Brad Maryan for attempting to recollect these species in the wild, and Ryan Ellis, Glenn Shea and Aaron Bauer for comments on the manuscript.

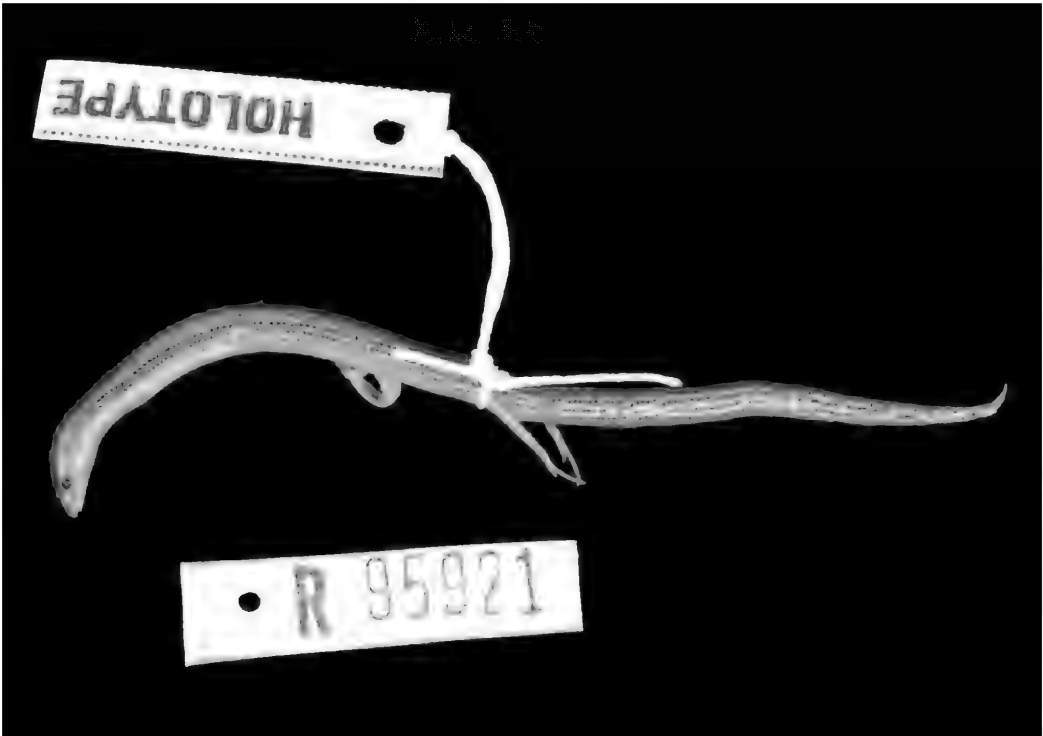


FIGURE 3 Holotype of *Lerista maculosa*. Note spotted appearance — the only presumed diagnostic character of this species.



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## SHORT COMMUNICATION

# Thirty-six years a synonym: the nomenclatural tale of the Pilbara blue-tailed skink, *Lerista chalybura* Storr, 1985 (Squamata: Scincidae)

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The Australian endemic skink genus *Lerista* was first proposed by Bell (1833), concurrent with the description of *Lerista lineata*, the earliest referred species of the genus. The genus is now represented by 104 taxa (comprising 97 species with 10 subspecies), the most recent of which was described by Amey et al. (2019) (*L. anyara*), and is second only to *Ctenotus* (with 116 taxa, comprising 107 species with 16 subspecies) in diversity. The highest diversity of *Lerista* occurs in Western Australia, with 74 taxa (68 species and 9 subspecies). This diversity is largely attributed to the taxonomic works of the late Glen Milton Storr (1921–1990), who, during his time as Curator of Ornithology and Herpetology at the Western Australian Museum (WAM), described a total of 42 currently recognised WA species ( $n = 36$ ) and subspecies ( $n = 6$ ) in published works between 1971 and posthumously to 1991.

In a revision of the *Lerista frosti* species complex in *Records of the Western Australian Museum*, Storr (1985) described a new uniquely coloured species from the Pilbara region of Western Australia, proposing the name *Lerista chalybura* for the population. The accompanying diagnosis for the species was entailed ‘A small slender *Lerista* with four fingers, four toes, movable eyelids, large ear aperture (about twice as large as nostril), comparatively long foreleg (more than 6 mm long in adults and subadults), greyish or bluish tail, and narrow, inferiorly ill-defined, dark upper lateral stripe’. The new species was described from 22 specimens, including the holotype (WAM R73934; Figure 1), 15 paratypes (R37078, R37087, R69727–29, R88824–32, R12387 and R73931–33 from WAM, R12594 from the South Australian Museum [SAMA] and R100608 from the Australian Museum [AMS]) and WAM R70741, which was excluded from the type series due to inconsistent variation with others in the type series. This specimen was later considered to represent another undescribed species, and Storr (1990) designated it as the holotype in the

description of *Lerista concolor* Storr, 1990 (now *Lerista quadrivincula* Shea, 1991, due to homonymy of the original name).

In their controversial self-published works printed the same year, Richard Wells and Ross Wellington proposed the name *Lerista zietzi* for the same population (Wells and Wellington 1985). The diagnosis presented by Wells and Wellington (1985) for *L. zietzi* essentially summarises features of three specimens detailed by Storr (1971) under geographic variation for *L. frosti*, to which the species was assigned. The two proposed new taxa are synonymous, particularly as the descriptions by Storr (1985) and Wells and Wellington (1985) share the same diagnostic information and some type material: the holotype of *L. zietzi* (WAM R37078; Figure 2), the only specimen mentioned by Wells and Wellington, is also a paratype for *L. chalybura*.

In accordance with Article 23 of the International Code of Zoological Nomenclature (the Code; International Commission on Zoological Nomenclature [ICZN] 1999), the valid name of a taxon is the oldest available name applied to it. The printed publication date for volume 12, issue 3 of the *Records of the Western Australian Museum* containing Storr (1985), is stated as ‘30 August 1985’. The *Australian Journal of Herpetology* supplementary series number 1 containing Wells and Wellington (1985) states on the front cover ‘Published 1 March, 1985’. Therefore based on the printed publication dates of the journal issues in which Storr (1985) and Wells and Wellington (1985) occurred, the Wells and Wellington name *Lerista zietzi* takes precedence over Storr’s *Lerista chalybura*, rendering *L. chalybura* a junior synonym of *L. zietzi*. While the Western Australian state government published *Records of the Western Australian Museum* printed publication dates are considered accurate, there has been uncertainty regarding the printed dates for the self-published *Australian Journal of Herpetology* and the supplementary series (Shea and Sadlier 1999; Aplin and Smith 2001).

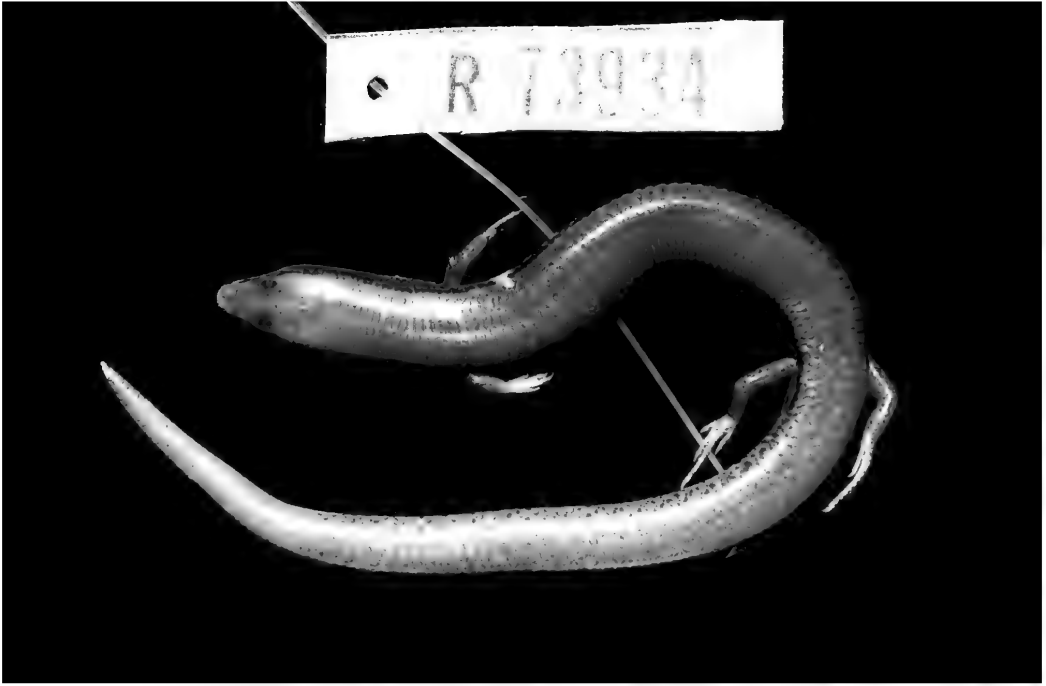


FIGURE 1 Holotype of *Lerista chalybura* Storr, 1985 (WAM R73934).



FIGURE 2 Holotype of *Lerista zietzi* Wells and Wellington, 1985 (WAM R37078)

Shea and Sadlier (1999) noted that they were unable to identify a copy of Wells and Wellington (1985) having been received prior to 19 September 1985, post-dating Storr (1985). As a result, they maintained the use of *L. chalybura* as the senior synonym, until the publication dates were more definitely assessed. Conversely, Aplin and Smith (2001) maintained the use of *L. zietzi*, following the nominal publication dates until Wells and Wellington (1985) were verified. Subsequently, despite *L. zietzi* generally receiving common usage, there has been inconsistent use of the two names and treatment of synonymy in publications to date. From 1985 to date (excluding publication of description), the name *L. zietzi* has been used a total of 24 times (Storr et al. 1999; Aplin and Smith 2001; Wilson and Swan 2003a,b; Amey et al. 2005; Clayton et al. 2006; Couper et al. 2006; Skinner 2007; Skinner et al. 2008; Wilson and Swan 2008; Australian Biological Resources Study 2009; Skinner and Lee 2009; Wilson and Swan 2009; Skinner 2010; Wilson and Swan 2010; Doughty et al. 2011; Wells 2012; Wilson and Swan 2013; Cogger 2014a,b; Wilson and Swan 2017; Cogger 2018; Wilson and Swan 2021; Macdonald 2022) compared to only 18 times for *L. chalybura* (Wilson and Knowles 1988; Storr 1990; Cogger 1992a,b; Ehmann 1992; Hutchinson 1993; Cogger 1994, 1996; Stanger et al. 1998; Shea and Sadlier 1999; Cogger 2000a,b; Meiri 2008; Australian Biological Resources Study 2010; Wilson et al. 2017; Chapple et al. 2019; Australian Society of Herpetologists Taxonomic Committee 2022; Uetz et al. 2022).

In a 2009 review of the scincid genera *Eulamprus* and *Glaphyromorphus*, conforming with Recommendation 21F of the Code (ICZN 1999), on 31 occasions when referencing Wells and Wellington (1985), Wells (2009) stated 'March 1985 on title page, but not published until September, 1985', confirming suspicions that the publication date on the cover was erroneous, whether due to a delay in publication or fabrication. Despite Wells (2009) stating the actual publication date, and technically rendering *L. zietzi* a junior synonym of *L. chalybura*, the inconsistent use of the two names has continued in subsequent publications, with 11 uses of *zietzi* (Skinner 2010; Wilson and Swan 2010; Doughty et al. 2011; Wells 2012; Wilson and Swan 2013; Cogger 2014a,b; Wilson and Swan 2017; Cogger 2018; Wilson and Swan 2021; Macdonald 2022) and five uses of *chalybura* (Australian Biological Resources Study 2010; Wilson et al. 2017; Chapple et al. 2019; Australian Society of Herpetologists Taxonomic Committee 2022; Uetz et al. 2022). This oversight by subsequent authors is presumably attributed to either consideration that the name was in relatively common usage, as to not disrupt widespread acceptance; unawareness of the publication in which Wells (2009) was published, given the journal was self-published and not widely disseminated; or a simple disregard of the author and/or the journal. The latter aligning with an attempted suppression of Well's nomenclatural works, including Wells and Wellington

(1985), by the broader herpetological community (Australian Society of Herpetologists 1987; ICZN 1991), particularly anything published after 2000, following Kaiser et al. (2013) who recommended that anything post-2000 not be treated as published nomenclatural works and be ignored. Although the nomenclatural actions of Wells (2009) pertaining to new names are not accepted following Kaiser et al. (2013), the information concerning the publication date of Wells and Wellington (1985) contained within it is published and not affected by either the Code or Kaiser et al. (2013), therefore applicable to the resolution of the correct publication date for *L. zietzi*.

Given that all type material assigned to *L. chalybura* and *L. zietzi*, particularly holotypes, share all morphological characteristics and in the absence of any evidence to suggest the holotype specimens represent different taxon, the two are considered to represent the same taxon. In conformance with the Principal of Priority (Article 23), based on the corrected publication date of September 1985 for Wells and Wellington (1985), it post-dates the Storr's 20 August 1985 published date, therefore *L. chalybura* is the earlier available name for the taxon. Despite more frequent use of *L. zietzi* since 1985 (24 v 18), maintenance of the junior synonym by way of prevailing usage under Article 23.9.1 of the Code (ICZN 1999) does not apply to the treatment of *L. zietzi* and *L. chalybura*. We hereby formally treat *Lerista zietzi* Wells and Wellington, 1985 as a junior synonym of *Lerista chalybura* Storr, 1985.

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# Middle Eocene echinoids from the western Eucla Basin, Western Australia

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**ABSTRACT** – The oldest carbonate sediments in the western Eucla Basin in south-western Australia are a series of cool-water bryozoan-dominated bioclastic grainstones, packstones and marls that represent deposition during the Tortachilla Transgression during the Bartonian (middle Eocene) planktonic foraminiferal zones 14–15. The two principal units are the Nanarup Limestone and a unit reported here for the first time and named, informally, the Manypeaks limestone. These units contain rich invertebrate faunas dominated by bryozoans, echinoids, bivalves and brachiopods. Herein we document fourteen echinoid species that occur in these limestones. They comprise one cidaroid, one camarodot, one salenioid, two cassiduloids, one echinolampadoid, one clypeasteroid and seven spatangoids. Four new species are described, the cassiduloid *Eurhodia westaustraliae* sp. nov., the clypeasteroid *Fossilaster susae* sp. nov., and the spatangoids *Cyclaster jamiei* sp. nov. and *Gillechinus kaitae* sp. nov. The species of *Fossilaster* represents the earliest known member of the Fossilasteridae and the earliest known record of a marsupiate echinoid in Australia. Analysis of the middle and late Eocene echinoids faunas of the western Eucla Basin establishes that the Nanarup Limestone echinoid fauna represents the cassiduloid biofacies, while the Manypeaks limestone is a mixed cassiduloid and spatangoid biofacies.

**KEYWORDS:** Echinoidea, Eocene, taxonomy, palaeoecology, Western Australia

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## INTRODUCTION

The Eucla Basin in southern Australia represents the largest tract of onshore Cenozoic marine sediments in the world (Clarke et al. 2003). It extends from the south-west corner of the continent near Albany in Western Australia, east for some 2,500 km to the St Vincent Gulf in South Australia. It spreads north about 350 km from the Great Australian Bight, while offshore it extends at least 500 km south of the present day coastline. Including its offshore extension it covers an area of more than one million square km, and as such covers about 15% of the Australian continent. Stratigraphically it is surprisingly uniform across its entire width, consisting of clastic and carbonate units ranging in age from middle Eocene to middle Miocene. These were deposited during a series of major transgressive events across the southern Australian continent, following the final separation of the Australian continent from Antarctica (Clarke et al. 2003; Hou et al. 2008).

This paper concerns the echinoid fauna from the western-most part of the basin. Formerly this area was considered to represent a separate, much smaller basin, the Bremer Basin. However, as Clarke et al. (2003) have argued, the continuous nature of the sedimentation across the entire southern part of the continental shelf at this time suggests they all form part of a single basin of deposition. The oldest Cenozoic rocks preserved in the western part of the Eucla Basin in south-western Australia consist of a sequence of Eocene sedimentary units (Figure 1): the North Royal Formation, overlain by the Nanarup Limestone, Werillup Formation and Pallinup Formation (Clarke et al. 2003). These are predominantly clastic units: sandstones, clays, siliceous spongolites and lignite-rich beds, apart from the Nanarup Limestone. This is one of a number of small, localised bryozoal limestone deposits in the area, within which the echinoids occur, and which may have been deposited as shoals on topographic highs.

These limestones are considered to correlate with the Norseman and Paling formations and the Wilson Bluff Formation in other parts of the Eucla Basin (Clarke et al. 2003), and with the Tortachilla Limestone in the St Vincent Basin in South Australia. These carbonate units were all deposited during planktonic foraminiferal zones P14–15, and are thus late Bartonian (middle Eocene) in age (Li et al. 2003). Their deposition along the southern Australian margin at this time occurred during the Tortachilla transgressive event (Clarke et al. 2003). This marks the initiation of carbonate deposition off the southern margin of Australia and correlates with the acceleration in the divergence of Australia from Antarctica.

The limestones of the Eucla Basin contain rich, predominantly invertebrate, faunas but, given the general lack of outcrops, these faunas are relatively poorly known. The Nanarup Limestone is the most westerly outcropping of these limestones and is the most accessible and extensively collected. Like the other Eucla Basin limestones, it is a typical cool-water carbonate (Boreen and James 1995), being dominated by bryozoans and echinoids, but also containing bivalves, gastropods, brachiopods, foraminifers, nautiloids, calcareous algae, asteroids, isocrinid and comatulid crinoids, sponges and crabs (McNamara 1992). Rare shark teeth also occur. Of these groups, only the

brachiopods (Craig 1997, 2001; Robinson 2017), the isocrinid crinoids (Whittle et al. 2018), palynomorphs (Hos 1975) and foraminifers (Quilty 1969, 1981) have been described.

Despite being a very common component of these bryozoal limestones, little has been written about any of the Eucla Basin Eocene echinoids. Philip (1970) figured, but did not describe, *Salinida* [sic] *tertiaria* (Tate) (= *Pleurosalenia tertiaryaria*) (Philip 1970, fig. 56B), *Brissopatagus cudmorei* (Fell) (= *Gillechinus susae* sp. nov.) (Philip 1970, figs 56F, 57D) and *Australanthus longianus* (Gregory) (Philip 1970, fig. 58B, E) from the Wilson Bluff Limestone. McNamara and Philip (1980a) discussed the occurrence of *Echinolampas posterocrassa* in the Nanarup Limestone, pointing out the similarities with penecontemporaneous material from the Tortachilla Limestone, some 2,500 km to the east. McNamara (1994a) recorded the occurrence of the marsupiate echinoid *Fossilaster* in the Nanarup Limestone, noting that it is the earliest record for a marsupiate echinoid in the Australian Cenozoic. Herein we document 14 species of echinoids: one cidaroid; one camarodont; one salenioid; two cassiduloids; one echinolampapoid; one clypeasteroid; and seven spatangoids, describing one new cassiduloid, one new clypeasteroid and two new spatangoid species. In addition to documenting this western Eucla

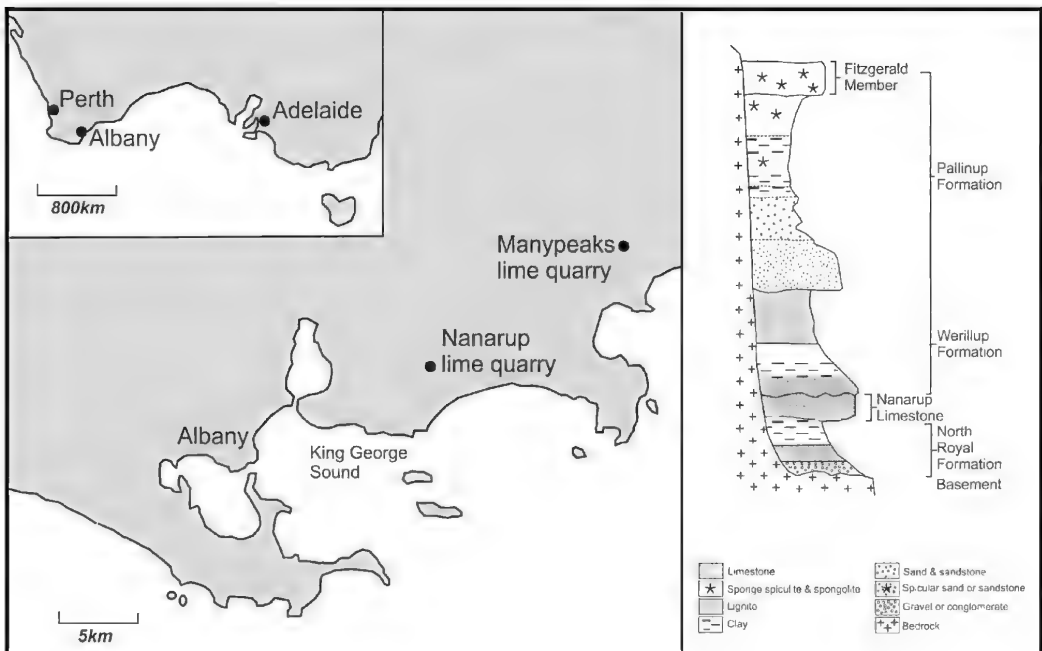


FIGURE 1 Map showing locations of the Nanarup and Manypeaks lime quarries in south-west Western Australia and chart of the middle and late Eocene stratigraphy of the western Eucla Basin (after Clarke et al. 2003). The Manypeaks limestone is contemporaneous with the Nanarup Limestone.



Basin middle Eocene echinoid fauna, we discuss its palaeoecological significance in terms of echinoid biofacies variability within different outcrops of the limestone and also compare it with the echinoid faunas from the younger Pallinup Formation in the western Eucla Basin and the coeval Tortachilla Limestone in the St Vincent Basin in South Australia.

#### GEOLOGICAL SETTING

This most westerly Eucla Basin echinoid fauna occurs mainly in two discrete limestones: the Nanarup Limestone and a more pelitic facies, informally named the 'Manypeaks limestone', which outcrops in a lime quarry 7 km south of Manypeaks township. The type Nanarup Limestone is only exposed in the Nanarup lime quarry, 17 km east of Albany, Western Australia at 118°02'45"E, 34°58'35"S (Figure 1). The limestone is about three metres thick in the quarry. A basal one metre of yellow, friable, medium-grained bryozoal grainstone is overlain by a one metre thick layer of white, finer, more silty packstone. The upper metre is similar in character to the lower, coarser-grained bed. The limestone was probably deposited in a shallow-water, open shelf environment.

A previously unrecorded coeval limestone is exposed in a small lime quarry located 20 km northeast of Nanarup at Manypeaks, at 118°12'00"E, 34°53'40"S. Here, a basal bed of brown bryozoal grainstone is overlain by a finer-grained pale grey-white packstone, with thin, interbedded green wackestone. This sequence is overall more finer-grained than at Nanarup and was probably deposited in slightly deeper water. It does not appear to be contiguous with the Nanarup Limestone and appears to be one of a series of discrete limestones that occur in the region (Clarke et al. 2003). The limestone unit has not been formally described. Herein we refer to it informally as the 'Manypeaks limestone'. A third, very small and very thin, outcrop occurs 16 km south-east of Manypeaks at Waychinacup Inlet. This bryozoal grainstone is lithologically similar to the Nanarup Limestone. The unit is referred to informally as the 'Waychinacup limestone'. It has only yielded a small number of cidaroid spines.

The Nanarup Limestone overlies a series of middle Eocene clastics and lignite of the North Royal Formation (Clarke et al. 2003) (Figure 1). It is overlain by the Werillup Formation, which Clarke et al. (2003, p. 241) have restricted to late Eocene clastics and lignite deposited in non-marine to marine environments. Formerly, the Nanarup Limestone had been regarded as a member of the Werillup Formation. However as Clarke et al. (2003, p. 240) have pointed out, it is a lateral equivalent to the limestones of the Norseman Formation and with further mapping warrants being elevated to the status of the Nanarup Formation. Herein we simply refer to it as the Nanarup Limestone. As we demonstrate, the close similarity of the echinoid faunas of the Nanarup Limestone and the Manypeaks limestone indicate they are coeval deposits.

#### MATERIAL EXAMINED

Excluding echinoid spines, 669 specimens were examined in this study, of which 627 were from the Nanarup Limestone, the rest from the Manypeaks limestone (for details see Table 1). 870 spines have been collected from the two limestones. Specimens used in this study are housed in the collections of the Western Australian Museum (WAM) and the Natural History Museum, London (NHM). In species descriptions test length is abbreviated to TL.

#### SYSTEMATIC PALAEOLOGY

**Class Echinoidea Leske, 1778**

**Order Cidaroida Claus, 1880**

**Family Cidaridae Gray, 1825**

**Subfamily Cidarinae Gray, 1825**

**Genus *Temnocidaris* Cotteau, 1863**

**Subgenus *Stereocidaris* Pomel, 1883**

#### TYPE SPECIES

*Cidaris cretosa* Mantell, 1835 [= *Cidaris sceptrifera* Mantell, 1822] by subsequent designation of Lambert and Thiéry (1909).

***Temnocidaris (Stereocidaris) cudmorei*  
Philip, 1964**

Figure 2

#### MATERIAL EXAMINED

**Australia: Western Australia:** Only incomplete cidaroid tests are known, including infrequent entire interambulacra and conjoined ambulacral plates, along with hundreds of random, single interambulacral plates. No complete specimens are known, nor specimens with attached apical zones. The following specimens from the Nanarup Limestone, Nanarup lime quarry, contain sufficient features to be assigned to this species: WAM 03.23, 03.24, 03.14–03.25, 07.426, 07.442 (36), 72.51[2], 76.87 (2), 76.88 (5), 88.853, 94.845 (8). Specimens from the Manypeaks limestone, Manypeaks lime quarry, include WAM 67.217–67.220, 69.255 (68), 76.90 (2), 76.91 (5), 94.812 (42), 94.813 (5), 94.846 (35), 03.55–03.71. None of the spines from either limestone is associated with coronal fragments.

#### REMARKS

Cidaroids are a common component of the Nanarup Limestone, less so in the Manypeaks limestone. Specimens are preserved both as incomplete tests and radioles (Figure 2). Test fragments occur commonly, including infrequently entire interambulacra and conjoined ambulacral plates, along with hundreds of

random, single interambulacral plates. No complete specimens are known, nor specimens with attached apical zones. Of the many hundreds of cidaroid radioles, none has been found with associated coronal fragments. The coronal specimens are identified as *Temnocidaris* (*Stereocidaris*) *cutdmorei* Philip, 1964. Philip (1964) described six species of *Stereocidaris* from the Tertiary of south-eastern Australia: *S. australiae* (Duncan, 1877), *S. cutdmorei* Philip, 1964, *S. fosteri* Philip, 1964, *S. inermis*, Philip, 1964, *S. (?) intricata* Philip, 1964 and *S. (?) hispida*. Many specimens from the Nanarup Limestone resemble *T. (Stereocidaris) cutdmorei*, others more closely resemble *T. (Stereocidaris) fosteri*. Both of these species occur in the middle Eocene Tortachilla Limestone in the St Vincent Basin, South Australia. Variation in the nature of the interambulacral plates in the Nanarup Limestone specimens shows that *T. (Stereocidaris) fosteri* should be considered a junior synonym of *T. (Stereocidaris) cutdmorei*. Tortachilla Limestone forms of *T. (Stereocidaris) cutdmorei* can possess up to nine interambulacral plates (Philip 1964). Most specimens from the Nanarup Limestone have up to seven, however, large specimens can have nine plates. The very common cidaroid radioles that occur in the Nanarup Limestone can be compared with

similar Cenozoic material from other middle Eocene deposits in southern Australia (Philip 1964), particularly *T. (Stereocidaris)* sp. A from the Tortachilla Limestone figured by Philip (1964, pl. LXI, figs 2 and 3).

Smith and Wright (1989) referred *T. (Stereocidaris) cutdmorei* to the latest Cretaceous to recent genus *Goniocidaris* due to 'test sculpturing identical to that found in *Goniocidaris* and its close relatives' (Smith and Wright, 1989, p. 44), despite preserving a rudimentary upper scrobicula, a feature lacking in *Goniocidaris*. Furthermore, we do not consider that the development of small pits at triple suture points is sufficient to rule out the placement of this species within the subgenus *Stereocidaris*.

Another character that supports this species inclusion in *Stereocidaris*, as Philip (1964) proposed, is the presence of wide pore pairs, and thus wide poriferous zones compared with the overall width of the ambulacra. These are typical *Stereocidaris* traits. In fact, Philip considered that the *Stereocidaris* species generally preserve poriferous zones that are marginally wider or equivalent in width to the interporiferous zones. The possession of wider poriferous than interporiferous zones is present in the Nanarup Limestone specimens — on average the interporiferous zone forms about two-fifths of the ambulacra (range one-third to one-half of ambulacral width).

Smith and Wright (1989) proposed the emplacement of *Stereocidaris* as a subgenus of *Temnocidaris* for all those species in which the uppermost scrobicula is rudimentary, the sculpture mild, and pedicellariae pits confined to the sutures. In addition, the absence of pits scattered amongst the interambulacral miliary tubercles is another characteristic feature of *Stereocidaris*. It should be noted that in their description of the subgenus *Stereocidaris*, Smith and Jeffery (2000, p. 26) consider the ambital and adapical plates need to be 'at least as tall as wide'. This character is present in most plates.

#### Order Camarodonta Jackson, 1912

#### Family Trigonocidaridae Mortensen, 1903

#### Genus *Ortholophus* Duncan, 1887

#### TYPE SPECIES

*Temnechinus lineatus* Duncan, 1877, by monotypy.

#### *Ortholophus* aff. *bittneri* Philip, 1969

#### MATERIAL EXAMINED

Fourteen whole or partial tests (WAM 03.26–03.39) from the Nanarup lime quarry, Nanarup Limestone. These are generally well preserved, although all lack the apical system. Two unregistered fragments, which may also belong to this species, are present in the Manypeaks limestone.

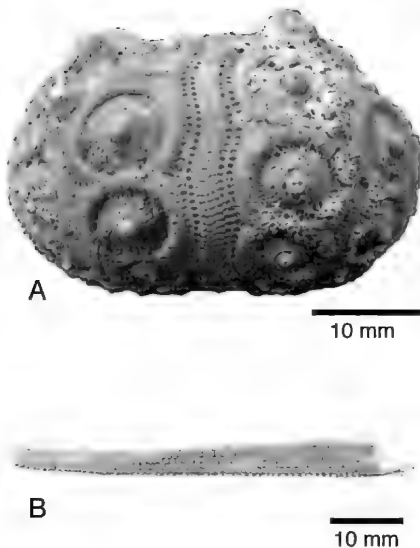


FIGURE 2 A) *Temnocidaris* (*Stereocidaris*) *cutdmorei* Philip, 1964, WAM 2022.165 from the Nanarup lime quarry, W.A., middle Eocene (Bartonian) Nanarup Limestone, incomplete test; B) *Temnocidaris* (*Stereocidaris*) sp., WAM 03.55 from Manypeaks lime quarry, W.A., middle Eocene (Bartonian) Manypeaks limestone, radiole.

## REMARKS

Due to the relatively indistinct test sculpturing in the Nananrup Limestone *Ortholophus* specimens, this species can be considered part of Philip's (1969) *O. woodsi* - *O. pulchellus* - *O. lineatus* species group. Philip (1969, p. 253) notes, however, that 'the differences [between species] are based on distinctions in the sculpture, and no fundamental characters permit separation of the species'. In spite of this, the *Ortholophus* species from the Nananrup Limestone differs from the late Miocene *O. lineatus* (Duncan, 1877), the early Miocene *O. venustus* Philip, 1969 and middle Miocene *O. morganensis* Philip, 1969 in possessing narrower ambulacra. It would be expected that the Nananrup Limestone form would be conspecific with the coeval *O. bitneri* Philip, 1969 from the Tortachilla Limestone in South Australia. However, this species often has a pentagonal test and preserves pore pairs sunken within the ornament surrounding the primary ambulacral tubercle. At this stage we prefer to regard the western Eucla Basin form as *Ortholophus* aff. *bitneri*.

**Order Salenioida Delage and Hérouard, 1903****Family Saleniidae L. Agassiz, 1838****Genus *Pleurosalenia* Pomel, 1883**

## TYPE SPECIES

*Salenia tertiaria* Tate, 1877, by original designation.

***Pleurosalenia tertiaria* (Tate, 1877)**

## MATERIAL EXAMINED

Single specimens are known from the Nananrup lime quarry, Nananrup Limestone (WAM 03.29) and the Manypeaks lime quarry, Manypeaks limestone (WAM 94.831).

## REMARKS

In addition to its type locality in the Tortachilla Limestone at Aldinga, South Australia (Tate, 1877), this species has also been recorded from the Wilson Bluff Limestone in the eastern Eucla Basin (Philip 1965). Its presence in the Nananrup Limestone and Manypeaks limestone extends its known range to the far western Eucla Basin.

**Order Cassiduloida Claus, 1880****Family Cassidulidae L. Agassiz and Desor, 1847****Genus *Eurhodia* Haime  
(in d'Archiac and Haime), 1853**

## TYPE SPECIES

*Eurhodia morrissi* Haime in d'Archiac and Haime, 1853, by original designation.

***Eurhodia westaustraliae* sp. nov.**

## Figure 3

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## MATERIAL EXAMINED

*Holotype*

**Australia: Western Australia:** WAM 07.439 from the middle Eocene (Bartonian) Nananrup Limestone at Nananrup lime quarry.

*Paratypes*

**Australia: Western Australia:** WAM 07.440 and 07.441 from the same locality and horizon as the holotype.

*Other material*

**Australia: Western Australia:** One additional, unregistered specimen from the Manypeaks limestone.

## DIAGNOSIS

Species of *Eurhodia* with elongate, narrow, low vaulted test; anal furrow narrow, reaching one-third test length and extending to ambitus, indenting ambital outline; periproct dorsal, inclined and longitudinal in furrow; peristome small, narrow, anterior; bourrelets weakly inflated; phyllodes small with eight single pores in each ambulacral column; ventral tubercles coarse; dorsal tubercles uniform and small.

## DESCRIPTION

Test elongate, elliptical; maximum length 36.5 mm. Widest part of test at about mid-test, maximum width 66%–68% TL. Anterior two-thirds of test rounded, posterior third tapers and truncated posteriorly. Test not highly inflated; maximum height 35–37% TL at roughly mid-test. No anterior notch. Apical system slightly anterior of mid-test; number of gonopores unknown. Posterior petals relatively long and narrow, not closed distally; anterior petals shorter. Poriferous and interporiferous zones are roughly equal in width; inner pores rounded and outer more elongate. Extra-petal pores present only in anterior ambulacrum. Periproct on aboral surface, set into the test at about 65° to adoral surface; forms an elongate ellipsoid and lies within triangular furrow in test that indents ambitus (Figure 3D); longer than wide (width 43–45% of length); length 10–15% TL.

Peristome small; anterior of mid-test, 37–38% TL from anterior; longer than wide, width being 84–87% of length; length 7–9% TL. Bourrelets weakly swollen, extending slightly across peristome, intruding enough to give peristome a stretched star shape (Figure 3B, E). Phyllodes small, with eight single pores in each row. Plastron extremely reduced and barely raised or distinguishable. Adoral surface concave, both longitudinally and laterally. Aborally, tubercles are developed evenly and uniformly over test surface; small and closely packed; sunken and symmetrical. Adorally,

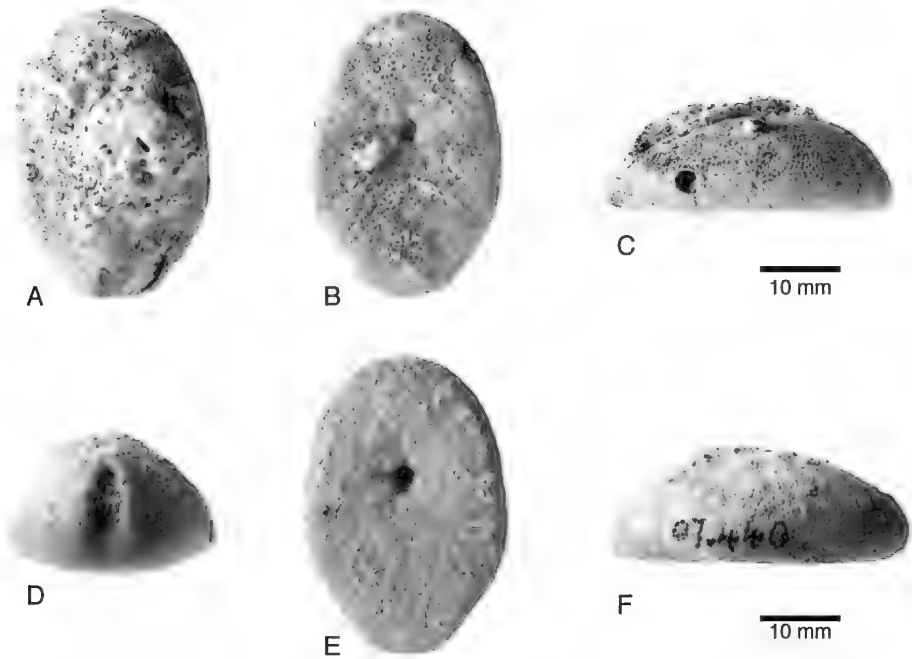


FIGURE 3 *Eurhodia westaustraliae* sp. nov. A–C, holotype WAM 07439 from the Nanarup lime quarry, middle Eocene (Bartonian) W.A., Nanarup Limestone: A) aboral; B) adoral; C) left lateral views. D–F, paratype WAM 07440 from the Nanarup lime quarry, W.A., middle Eocene (Bartonian) Nanarup Limestone: D) posterior; E) adoral; F) right lateral views.

tubercles larger, with aureoles surrounded by a raised rim making them appear inset, and having large boss in relation to areole size (Figure 3B); asymmetrical, indicating a stroke towards posterior of test.

#### REMARKS

Three morphological features change with increasing test length. The first is a relative decrease in peristome width in relation to its length, and thus a change towards a more equant peristome with increasing test length. The second is a corresponding increase of peristome length in relation to test length, while the last is an increase of periproct length in relation to test length.

*Eurhodia westaustraliae* differs from *E. australiae* (Duncan, 1877) from the contemporaneous Tortachilla Limestone in a number of features. Most noticeable is the shape of the test, which is much narrower and relatively more elongate in *E. westaustraliae*. On the basis of the measurements given by Duncan (1877, p. 51) for the holotype (NHM GSL 14079), from the Castle Cove Limestone in Cape Otway (Victoria), and two specimens from the Tortachilla Limestone also in the Natural History Museum, London collections (NHM E74558, 74559), the standardised test width for *E. australiae* is 70–75% TL, whereas for *E. westaustraliae*

it is 66–68%. Adorally, the peristome is relatively smaller and narrower in *E. westaustraliae*. Similarly, the phyllode is relatively smaller, with only eight single pores in each ambulacral column, compared with 11 in *E. australiae* (<http://www.nhm.ac.uk/research-curation/research/projects/echinoid-directory/taxa/specimen.jsp?id=7587>).

There are also some differences in the tuberculation. Duncan (1877, p. 51) pointed out that the tuberculation in *Eurhodia* was 'small everywhere, and smallest in the anal groove'. *E. westaustraliae* has uniform tubercles aborally, but adorally the tubercles are generally much larger and more distinctive. He also described the anal furrow as almost reaching the test vertex, whereas *E. westaustraliae* has an anal furrow that reaches no more than one-third of the way towards the middle of the test. Thirdly, the anal furrow in *Eurhodia australiae*, while reaching below the level of the ambitus, does not affect the ambitus shape. In *E. westaustraliae*, however, the furrow reaches below the ambitus and does affect the shape, creating a small notch.

#### ETYMOLOGY

With reference to its occurrence on the western side of the Australian continent.

## Family Faujasiidae Lambert, 1905

Genus *Australanthus* Bittner, 1892

## TYPE SPECIES

*Cassidulus longianus* Gregory, 1890, by original designation.

## EMENDED DIAGNOSIS

Test oval; monobasal apical system with four gonopores; petals open, short, broad with narrow interporiferous tract and widely spaced conjugate poriferous zones with outer pore very elongate, inner rounded. Periproct supramarginal, longitudinal, narrow. Peristome pentagonal. Bourrelets strongly inflated. Phyllodes broad, with few single pores. Interambulacrum V broad and naked adorally.

*Australanthus longianus* (Gregory, 1890)

Figures 4G–I

*Cassidulus longianus* Gregory, 1890: 482, plate 13, figures 1–3.

*Cassidulus longianus* Gregory: Gregory 1892: 275; Tate 1892: 192

*Australanthus longianus* (Gregory); Bittner 1892: 349–352, plate 3, figure 2; Clark 1946: 375; Mortensen 1948: 222, figure 200a–b; Kier 1962: 151–2, plate 27, figures 1–4; Philip 1970: 183, figures 58B, E.

*Procassidulus (Australanthus) longianus* (Gregory), Lambert and Thiéry 1921: 363.

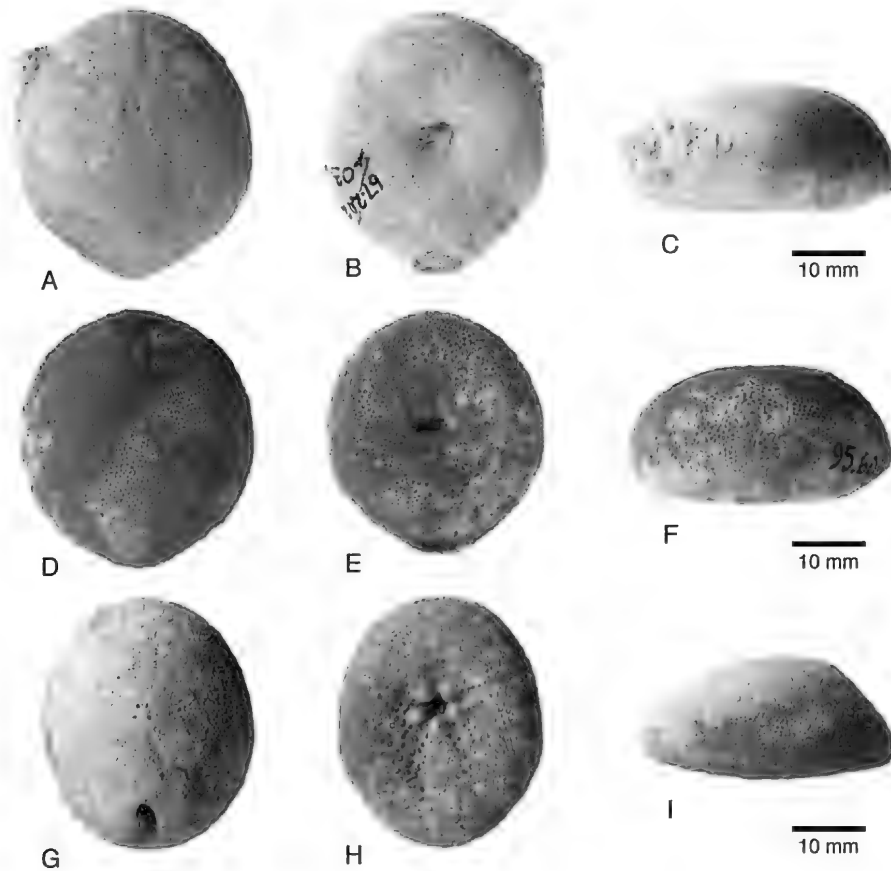


FIGURE 4 *Echinolampas posterocrassa* Gregory (1890). A–C, WAM 03.40 from the Nanarup lime quarry, W.A., middle Eocene (Bartonian) Nanarup Limestone: A) aboral; B) adoral; C) left lateral views. D–F, WAM 95.600 from Manypeaks lime quarry, W.A., middle Eocene (Bartonian) Manypeaks limestone: D) aboral; E) adoral; F) left lateral views. *Australanthus longianus* Gregory (1890). G–I, WAM 03.48 from Nanarup lime quarry, W.A., middle Eocene (Bartonian) Nanarup Limestone: G) aboral; H) adoral; I) left lateral views.

## MATERIAL EXAMINED

**Australia: Western Australia:** One whole, 17 partial and four fragmentary specimens (including WAM 03.47–03.49, 07.435–07.438, 72.53 [2]) from the Nanarup lime quarry, Nanarup Limestone. Three incomplete specimens from the Manypeaks lime quarry, Manypeaks limestone (WAM 03.11), none of which preserve dorsal features.

## REMARKS

The most common cassiduloid in the Nanarup Limestone is *Australanthus longianus* Gregory, 1890 (Figure 4G–I). Originally described from the Tortachilla Limestone, this species of *Australanthus* possesses a long, narrow, sunken periproct; a strongly demarcated, unornamented strip of plastron; an anal furrow that affects the ambital outline; and a well-developed floscelle (Figure 4H). The bourrelets of the Nanarup Limestone form are slightly less prominent and more rounded than in many toptype specimens, but are still distinct and compare well with Gregory's (1890, pl. 13, fig. 2) figured *A. longianus*.

A lectotype is herein selected for *Australanthus longianus*. The material upon which Gregory based the species was collected in the early 1880s by Harry P. Woodward, then Assistant Government Geologist in South Australia, from 'Willunga', South Australia and sent by him to the then British Museum (Natural History),

now the Natural History Museum, where his father, Henry Woodward, was the Keeper of Palaeontology. One of Gregory's described specimens is herein designated as the lectotype of the species, NHM E42428 (Gregory 1890, pl. 13, figs 1, 3) and specimens E42429 (Gregory 1890, pl. 13, fig. 2) and E42430, also used in Gregory's species description, designated as paralectotypes.

In addition to occurring in the Tortachilla, Nanarup and Manypeak limestones, *A. longianus* is also present in the contemporaneous Kingscote Limestone on Kangaroo Island, South Australia and in the Wilson Bluff Limestone in Western Australia (Philip 1970, fig. 58B, E). When specimens of the species are compared across its extensive palaeogeographic range of some 2,500 km, there are certain noticeable variations. Specimens are larger in the eastern part of the range. For example, eight specimens from the Kingscote Limestone reach up to 79 mm in test length, compared with 55 mm for the largest from the Nanarup Limestone. There is also a well-developed cline in shape and size of the peristome. In the eastern part of the range the peristome is much narrower, with most specimens having a peristome about half as wide as long. In the geographically intermediate Wilson Bluff Limestone from the Eucla Basin the peristome width is usually more than half the length. However, in the western most part of the range, in the Nanarup and Manypeak limestones, the peristome is almost as wide as long (see Figure 5). Moreover, there is a proportionate increase in peristome size along the cline. However, we consider that it would be unwise to differentiate these forms taxonomically, preferring to regard them as an example of a geographic cline.

**Order Echinolampadoida  
Kroh and Smith, 2010**

**Family Echinolampadidae Gray, 1851a**

**Genus *Echinolampas* Gray, 1825**

## TYPE SPECIES

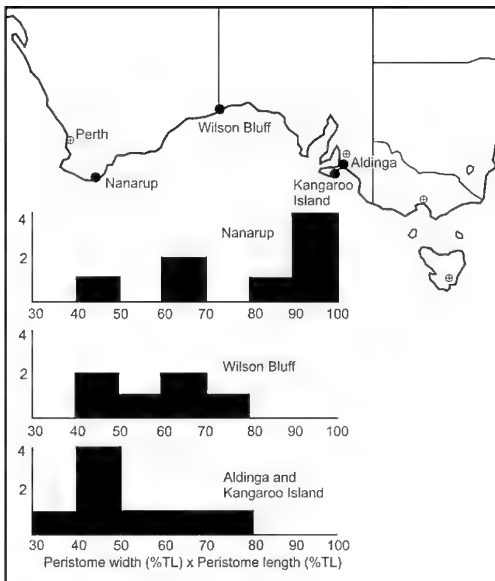
*Echinanthus ovatus* Leske, 1778, by subsequent designation of Pomel (1883).

***Echinolampas posterocrassa* (Gregory, 1890)**

Figures 4A–F

## MATERIAL EXAMINED

**Australia: Western Australia:** A total of 36 complete and 339 partial specimens from the Nanarup lime quarry, Nanarup Limestone (including WAM 67.202[5], 67.203, 67.204, 67.216[2], 69.256[7], 69.257, 70.184, 70.185, 70.186, 75.44[5], 75.45, 76.89[2], 03.40–03.46, 03.72[18], 03.73[57]). The species also occurs in the Manypeaks limestone in the Manypeaks lime quarry, although it is much rarer, with just one complete (WAM 95.600) and three partial specimens (WAM 95.601, 94.829 and 07.424).



**FIGURE 5** Histograms showing peristome shape of *Australanthus longianus* changing along a cline from the western Eucla Basin in Western Australia, east to the St Vincent's Basin in South Australia, showing a progressive widening from east to west.

## REMARKS

*Echinolampas posterocrassa* Gregory, 1890 (Figure 4A–F) is by far the most common echinoid in the Nanarup Limestone. This species is also a common component of the Tortachilla Limestone in the St Vincent Basin in South Australia (McNamara and Philip 1980a). Specimens from the Nanarup and Manypeaks limestones compare very closely with the topotype material. As McNamara and Philip (1980a, p. 3) have noted, the only difference between them is that specimens from the Nanarup and Manypeaks limestones have a slightly flatter test. This is not considered sufficient reason to propose yet another species of *Echinolampas*. During its ontogeny the Nanarup Limestone *E. posterocrassa* became less tumid. This is also seen in topotype material, but relative reduction in test height is greater in Nanarup Limestone specimens. Moreover, as the test increases in size the peristome becomes relatively wider, as does the periproct.

**Order Clypeasteroida A. Agassiz, 1872****Suborder Clypeasterina A. Agassiz, 1872****Family Fossulasteridae  
Philip and Foster, 1971**

## INCLUDED GENERA

*Fossulaster* Lambert and Thiéry, 1925 [= *Prowillungaster* Wang, 1994]; *Scutellinoides* Durham, 1955; *Willungaster* Philip and Foster, 1971; *Philipaster* Wang, 1994 [= *Orbispala* Irwin, 1995].

## EMENDED DIAGNOSIS

Small, flattened clypeasteroids; apical system with four or five genital pores; periproct supramarginal. Interambulacra discontinuous, not extending onto oral surface; demiplates absent from petaloid ambulacra; petals absent or poorly defined; auricles separate. Oral surface concave; primordial interambulacra greatly reduced; no combed areas; food grooves absent.

## REMARKS

When Philip and Foster (1971) first proposed the family Fossulasteridae it was based on three genera: *Fossulaster*, *Scutellinoides* and *Willungaster*. Since then, three further genera, *Prowillungaster*, *Philipaster* and *Orbispala* have been described (Wang 1994; Irwin 1995). As discussed below, *Prowillungaster* is herein considered to be a junior synonym of *Fossulaster*. *Orbispala* is considered a junior synonym of *Philipaster* (Smith and Kroh 2011). This form, unlike other fossulasterids, does not appear to be marsupiate. Durham (1955, 1966) placed *Scutellinoides* in the Arachnoididae, but Philip and Foster (1971) observed that it lacked pseudocompound plates and so erected the Fossulasteridae to include those genera that possessed separate auricles and simple plates in the petaloid ambulacra.

Irwin (1995) placed *Scutellinoides* in a new family, the Scutellinoididae. He considered that the presence of five gonopores and unique development of radial internal supports, besides the interradian and concentric partitions, formation of multiple minute clustered hydropores and lack of ambulacral petals were grounds for separating *Scutellinoides* from the Fossulasteridae and erecting the Scutellinoididae. However, the differences between *Scutellinoides* and other members of the Fossulasteridae are relatively insignificant and we follow Philip and Foster (1971) in placing it in the Fossulasteridae, considering Scutellinoididae as junior synonym of Fossulasteridae.

**Genus Fossulaster  
Lambert and Thiéry, 1925**

*Fossulaster* Lambert and Thiéry, 1925: 577.

*Prowillungaster* Wang, 1994: 229. New synonymy.

## TYPE SPECIES

*Fossulaster halli* Lambert and Thiéry, 1925, by original designation.

## REMARKS

Wang (1994) was incorrect in saying *Fossulaster* lacks aboral interambulacral plates. They are present and reach the ambitus, as in his *Prowillungaster*. Consequently, there is nothing to justify the retention of *Prowillungaster*. It is herein regarded as a junior subjective synonym of *Fossulaster*.

***Fossulaster susae* sp. nov.**

Figure 6

urn:lsid:zoobank.org:act:402C3BF6-C8F5-42D0-9B8D-DD5C69586845

## MATERIAL EXAMINED

*Holotype*

**Australia: Western Australia:** WAM 07.364 from the middle Eocene (Bartonian) Nanarup Limestone at Nanarup lime quarry.

*Paratypes*

**Australia: Western Australia:** WAM 07.330, 07.342, 07.357, 07.358 from the same locality and horizon as the holotype.

*Other material*

**Australia: Western Australia:** WAM 07.320–07.329, 07.331–07.341, 07.343–07.356, 07.359–07.363, 07.365–07.400. In addition to the type material there are eight specimens from the Manypeaks quarry, WAM 94.811[6], 94.833[2]. Of these, two are essentially complete, while the remaining are partial tests.

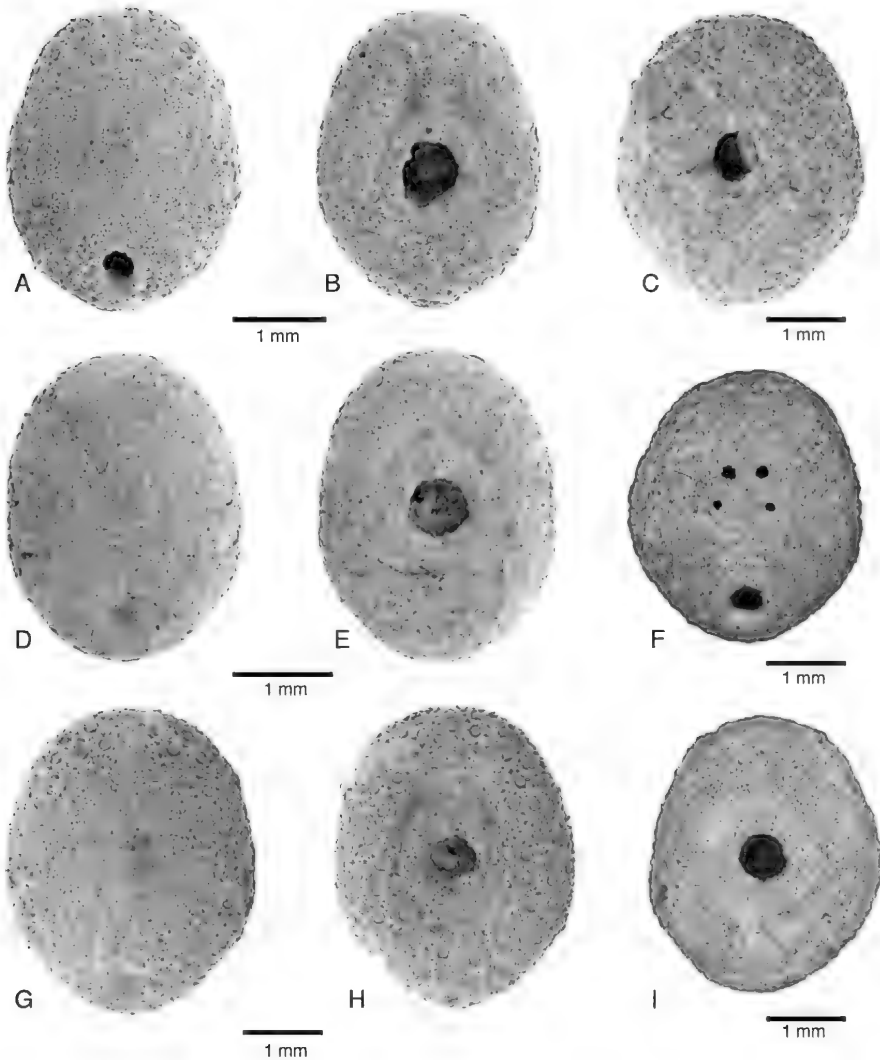


FIGURE 6 *Fossilaster susae* sp. nov. A–B, holotype WAM 07364 from the Nanarup lime quarry, W.A., middle Eocene (Bartonian) Nanarup Limestone: A) aboral; B) adoral views. C, paratype WAM 07358 from same locality and horizon as holotype: C) adoral view. D–E, paratype WAM 07342 from same locality and horizon as holotype: D) aboral; E) adoral views. F, I, paratype WAM 07330 from same locality and horizon as holotype: F) aboral; I) adoral views. G–H, paratype WAM 07357 from same locality and horizon as holotype: G) aboral; H) adoral views.

#### DIAGNOSIS

Very small species of *Fossilaster* with elongate, narrow test; shallow, bilobed marsupium; no anterior bulge on aboral surface.

#### DESCRIPTION

Test very small with a maximum known test length of 5.2 mm; average length 3.19 mm ( $n=61$ ); rounded to sub-pentagonal in shape. Smallest preserved specimen 1.21 mm long. Test width averaging 82% TL, ranging

from 74–92% ( $n=52$ ); maximum width just posterior of mid-test, averaging 64% TL ( $n=29$ ); relatively highly vaulted, with the average height just 37% TL, ranging from 39% TL to 54% TL. Aboral surface convex with well-rounded ambitus. Test outline rounded, with posterior slightly narrower than anterior. Aborally, interambulacra tend to be either narrower or equivalent in width to ambulacra (Figure 6D). Apical system on raised, rounded to pentagonal monobasal disc, on which gonopores are situated at edges (Figure 6F); positioned



posterior of mid-test, with front of anterior gonopores occurring on average 37% TL from anterior margin. Four gonopores, of which either anterior or posterior pair can be enlarged. However, this enlargement does not occur in all specimens and tends to be more common in larger than smaller individuals. Ambulacral pore pairs not apparent. No visible hypopores are present. Food grooves are lacking.

Peristome anterior of centre of test, averaging 41% TL from anterior (27–50% TL,  $n=66$ ); generally rounded, but almost pentagonal in some specimens. On average peristome slightly longer than wide, average peristome length being 21% TL (10–49% TL,  $n=70$ ). Relative size of peristome (both length and width) decreases appreciably as test length increases, with peristome width ranging from 49% TL in small specimens to only 10% TL in larger specimens. Some specimens possess a marsupium (Figure 6B, E, H), which forms around the anterior of rounded peristome, and causes peristome to develop a raised ring. Ventral surface of test concave, with most specimens having an inset peristome.

Periproct on dorsal surface of test near tapered posterior (Figure 6A). Rounded to teardrop shaped, average length and width 11% TL (7–21% TL,  $n=60$ ). Like peristome, periproct becomes relatively smaller as test length increases. It also migrates closer to test margin with this length increase. On average, periproct lies 27% TL from posterior margin (16–54% TL,  $n=58$ ). Test covered by a number of tubercles that are very coarse for the test size. These are developed everywhere except on apical disc, including within inset peristome / marsupium.

#### Sexual dimorphism

*Fossulaster susae* displays sexual dimorphism, similar to that observed in other species in the genus. As Smith (1984) suggests, it can be assumed that the presence of gonopores in a specimen indicates that the individual had attained sexual maturity. Thus, those well-preserved individuals lacking visible gonopores are considered to be juveniles, whereas those preserving gonopores are adult specimens. Female specimens are generally identified by the presence of a marsupium situated anterior of the peristome. In the largest specimens this marsupium is clearly seen, and develops a low divide, making the depression bilobed, not U-shaped (Figure 6B). In smaller specimens, however, the marsupium is much less developed. There appears to be no fixed size above which juveniles reached maturity, but the transition generally occurred at a test length of between 2.5 mm to 3 mm, with the smallest mature specimen being 2.4 mm, and the largest juvenile 2.8 mm.

Other sexually dimorphic features are apparent in *F. susae*. The width between the anterior gonopores, as a percentage of test length, does differ between genders, as based on the presence or absence of a marsupium, with the anterior gonopores being more widely spaced in forms lacking a marsupium than those with a marsupium. Marsupiate forms generally develop narrower, less rounded tests than non-marsupiate

forms. Marsupiate forms also tend to be slightly larger than non-marsupiate forms (average TL of 3.8 mm, compared with 3.5 mm). Non-marsupiate specimens tend to be slightly higher vaulted than marsupiate forms (average test height 33.4% TL, compared with 37.0% TL). Marsupiates are slightly more common than non-marsupiates, 59% compared with 41% male ( $n=51$ ).

In most sexually dimorphic echinoids, individuals with larger gonopores are considered to be female (Smith, 1984; Néraudeau 1993). Surprisingly, in *F. susae* there appears to be little positive relationship between the size of the anterior gonopores and the presence of a marsupium, as large gonopores can be found on specimens both with and without a marsupium (Figure 6F, I). This could indicate that, if indeed specimens with large gonopores are accepted as being female, then they failed to develop a marsupium. Frequently, individuals with very small gonopores, generally accepted as being males, possess a marsupium (see Figure 6A–B). This raises the intriguing possibility that in some of these earliest known brooding echinoids, the young may actually have been brooded by males.

#### REMARKS

The nature of preservation at Nanarup, where there has been some recrystallization, does not encourage the preservation of visible plate structure, leading to difficulties in determining some important test features. Although few plating structures are visible, the ambulacra appear to pass the ambitus and continue onto the ventral side, indicating that these specimens belong to *Fossulaster*, not *Willungaster*. The coarse, oversized tubercles and more elongate shape of *Fossulaster* also support this inference. However, the shallow marsupium is more like *Willungaster*, and quite different from the deep, distinctive marsupia seen in the other *Fossulaster* species (see Philip and Foster, 1971).

Of the three known species of *Fossulaster*, *F. exiguus* Philip and Foster 1971, from the early Miocene Melton Limestone of the St Vincent Basin, is the closest in size (less than 8 mm), but develops a U-shaped, not bilobed marsupium. *F. halli* Lambert and Thiéry 1925, from the Oligocene to early Miocene horizons of the Gambier (west Otway Basin) and Port Vincent (St Vincent Basin) Limestones, is the largest of the species with a test length up to 10 mm. Although it develops a bilobed marsupium like the Nanarup *Fossulaster*, the female specimens also develop an anterior dorsal bulge that is not seen in this smaller species. An undescribed form from the Oligocene to early Miocene Gambier Limestone of the west Otway Basin (P. Irwin pers. com.), also has a bilobed marsupium, grew up to 8.7 mm in length and has gonopores occurring peripheral on the apical disc. However, it has juveniles in which the periproct is more marginal than in *F. susae* and it too has an anterior dorsal bulge in the females. The lengths at the onset of maturity for the species are *F. halli* – 6.5 mm, *F. exiguus* – 4.5 mm, *Fossulaster* sp. (Gambier Limestone) – 5.5 mm and *F. susae* – 2.5–3.0 mm. *F. susae* is late middle Eocene in age, whereas the

other species range in age from the early Oligocene to Miocene. As such, *Fossilaster susae* represents the earliest known species of *Fossilaster*.

The presence of *Fossilaster susae* was first recorded by McNamara (1994a) who documented the occurrence of this, the first known marsupiate species in the Australian Cenozoic, in the middle Eocene Bartonian Stage (planktonic foraminiferal zones 14–15). Clypeasteroids do not appear in the eastern Australian Cenozoic sedimentary basins until the latest Oligocene/early Miocene, in the form of species of *Monostychia* (Sadler et al. 2016). None occur in the coeval Tortachilla Limestone, with which the Nanarup Limestone shares many species in common. However, one middle Eocene clypeasteroid has been recorded in the Giralia Calcarene in the Carnarvon Basin in north-west Australia, an undescribed species of *Monostychia* (McNamara 1999). This is of similar age to the middle Eocene new species of *Fossilaster* in the Nanarup Limestone and Manypeaks limestone described herein.

*Fossilaster susae* is one of the smallest known marsupiate echinoids, reaching a maximum known test length of just 5.2 mm, being exceeded only by the living *Fibularia nutriens*, which grows to no more than 3.3 mm in length (Mortensen 1948).

#### ETYMOLOGY

Named after Sue Radford in recognition of her assistance over many years not only in helping to collect the Nanarup Limestone echinoid fauna, but also in collecting many other fossil specimens now housed in the Western Australian Museum.

### Order Spatangoida Claus, 1876

#### Suborder Micrasterina Fischer in Moore, 1966

#### Family Micrasteridae Lambert, 1920

#### Genus *Cyclaster*

#### Cotteau in Leymerie and Cotteau, 1856

#### TYPE SPECIES

*Cyclaster declivus* Cotteau in Leymerie and Cotteau, 1856, by original designation.

#### *Cyclaster jamiei* sp. nov.

Figure 7

urn:lsid:zoobank.org:act:77D31A89-0578-4E2B-AD6A-79E570AC4CC2

#### MATERIAL EXAMINED

##### *Holotype*

**Australia: Western Australia:** WAM 03.12 from the middle Eocene (Bartonian) Manypeaks limestone in the Manypeaks lime quarry.

##### *Paratypes*

**Australia: Western Australia:** WAM 07.425, 07.432, 07.433 from the middle Eocene (Bartonian) Nanarup Limestone at Nanarup lime quarry.

##### *Other material*

**Australia: Western Australia:** WAM 89.1235 from the middle Eocene (Bartonian) Giralia Calcarene, Giralia Range, W.A. WAM 76.16, from the late Eocene (Priabonian) Pallinup Formation.

#### DIAGNOSIS

Species of *Cyclaster* with elongate, tapering, inflated test; anterior notch absent; no peripetalous fasciole; short, open, weakly bowed petals; elongate pore pairs; small, longitudinal, marginal periproct; anteriorly placed, small, transverse peristome with distinct labrum.

#### DESCRIPTION

Test up to 41 mm in length, with maximum width about 87% TL; greatest at anterior of test; maximum test height 72% TL developed mid-test, posterior of apical system; rounded anterior, tapering rapidly to an almost truncate posterior. No anterior notch. Well-developed keel runs from behind apical system posteriorly through interambulacrum 5. Apical system slightly sunken; anterior of mid-test, about 40% TL from anterior; three gonopores; ethmophract, with genital plates 1, 3 and 4 meeting mutually; genital plate 2 small and in contact with genital plates 1 and 4. Genital plate 2 with a number of hydropores, sparsely distributed, but lacking gonopore. Petals slightly sunken. Posterior pair slightly shorter than anterior pair, being about 21% TL; open distally; slightly shallower than anterior petals; anterior petals 22% TL. Pore pairs generally elongate. About 20 pore pairs in each anterior row in each petal. Ambulacrum III as sunken as anterior petals (Figure 7A); pore pairs widely spaced, strongly oblique with weak interporal partition. Peripetalous fasciole absent. Distinct subanal fasciole; reniform and relatively narrow, 37% TL; fasciole relatively broad, 3% TL.

Peristome small, wider than long, semicircular; length 68% of width; width about 11% TL; completely encircled by narrow, raised ridge (Figure 7E). Anterior of peristome lies close to test anterior, at around 22% TL. Labrum is extremely long and thin, parallel-sided, about 20% TL. Not anteriorly projecting. Ambulacrum III weakly sunken adorally. Pores in phyllode with prominent interporal partitions. Periproct high on inflated, truncated posterior; small and roughly tear-shaped (Figure 7F). Slightly longer than wide (width 87% of length), length about 10% TL. Plastron weakly developed.

Tubercles on aboral surface uniformly small, but evenly distributed, while adoral interambulacral tubercles are larger and sparser. Small granules surround all larger 'primary' tubercles, thus no surfaces densely tuberculated. All areoles symmetrical. Aboral tubercles restricted to interambulacra and are so dense that plating arrangements in these areas generally obscured.

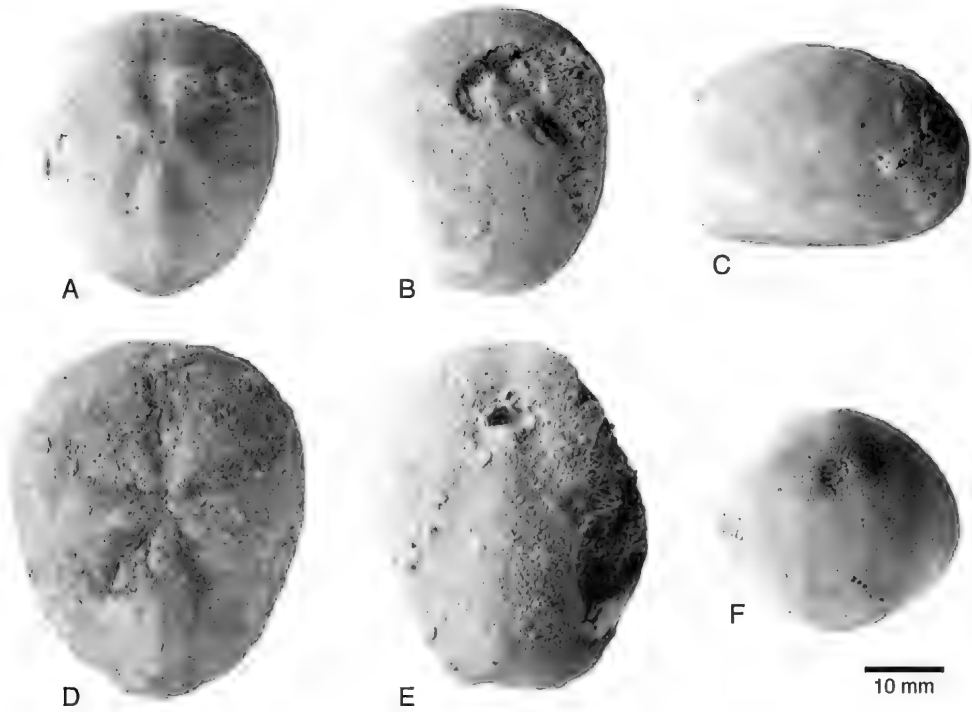


FIGURE 7 *Cyclaster jamiei* sp. nov. A–C, F, holotype WAM 03.12 from the Manypeaks lime quarry, W.A., middle Eocene (Bartonian) Manypeaks limestone: A) aboral; B) adoral; C) right lateral; F) posterior views. D) WAM 89.1235 from the middle Eocene Giralia Calcarenite, Giralia Range, W.A., aboral view. E) paratype WAM 07.425 from the Nanarup lime quarry, W.A., middle Eocene (Bartonian) Nanarup Limestone, adoral view.

Intrapetalous zones clear of primary tubercles. Posterior adoral ambulacra lack primary tubercles and ornamented only by dense granules. Plastron with large, densely packed tubercles, not interspersed with granules, with asymmetrical areoles indicating a sediment movement inwards and towards posterior.

#### REMARKS

As McNamara (1999) has previously reported, the same species of *Cyclaster* that occurs in the Nanarup and Manypeaks limestones, i.e., *Cyclaster jamiei*, also occurs in the middle Eocene of the Carnarvon Basin, where it is present in the Giralia Calcarenite (Figure 7D). Here it occurs in slightly older strata than the Nanarup Limestone, being, upper Zone P12 in age (Haig et al. 1997). *C. jamiei* has a more elongate, narrower, test than *C. archeri* (Tenison Woods, 1867), which is from the late Oligocene to middle Miocene Morgan Limestone, Gambier Limestone and Port Willunga Formation of the Murray and St Vincent Basins (McNamara et al. 1986, fig. 9). Its test width is 87% TL, compared with 89–99% TL in *C. archeri*. More notably, *C. jamiei* lacks a peripetalous fasciole. Smith and Kroh (2011) have noted that this fasciole may be complete, partial or completely absent in *Cyclaster*. *C. jamiei*

has less bowed anterior petals than *C. archeri*. While both species possess an ethmophract apical system, *C. archeri* has a more elongate genital plate 2, and has this plate in contact with all other genital plates (genitals 1 and 3 do not touch). In *C. jamiei*, however, genital 2 is only in contact with genital plates 1 and 3, and lies outside the mutual ring formed by the gonopore-bearing plates.

*Cyclaster jamiei* differs from the type species, *C. declivus* Cotteau, 1856 from the Eocene of France, by its narrower, more tapering test; lack of peripetalous fasciole in adults; more anteriorly positioned apical system; and shorter, shallower petals. *C. jamiei* also shares some similarities to a number of European *Cyclaster* species from the Cretaceous and Paleocene. In particular, it shares its lack of peripetalous fasciole with *C. aturicus* (Seunes, 1888), *C. suecicus* (Schlüter, 1897) and *C. ruegensis* (Kutscher, 1978) (Smith and Jeffery, 2000), but differs from them in lacking a prominent anterior notch and in the form of the petals.

#### ETYMOLOGY

Named after Jamie McNamara in recognition of his assistance in helping to collect the Nanarup Limestone echinoids and for collecting many specimens now housed in the Western Australian Museum.

**Genus ?*Isaster* Desor, 1858**

## TYPE SPECIES

*Isaster aquitanicus* Desor, 1858, by original designation.

**?*Isaster* sp.**

## MATERIAL EXAMINED

**Australia: Western Australia:** Two incomplete specimens, WAM 94.1340 and 03.52 from the Nanarup lime quarry, Nanarup Limestone.

## REMARKS

These two specimens share features reminiscent of *Isaster*, a Maastrichtian to Paleocene micrasterid that has previously been recorded from Kazakhstan, Ukraine, Turkey and Spain. Like *Isaster*, the Nanarup Limestone specimens have an ovate, domed test without an anterior sulcus; short, weakly developed petals; periproct on a truncate posterior margin and no peripetalous or lateroanal fascioles. They differ from described species of *Isaster* in possibly having a subanal fasciole, although this is not completely certain. The presence of *Isaster* in the Eucla Basin, if confirmed, would greatly extend the geographic range of this genus to the eastern Tethys and the stratigraphic range to the Eocene. Superficially the Nanarup Limestone specimens resemble *Prenaster aldingensis* Hall, 1906 from the Tortachilla Limestone and the slightly younger Pallinup Formation. However, unlike ?*Isaster* sp., this species possesses both a peripetalous and lateroanal fasciole (Hall 1906, pl. 13, figs 3–4).

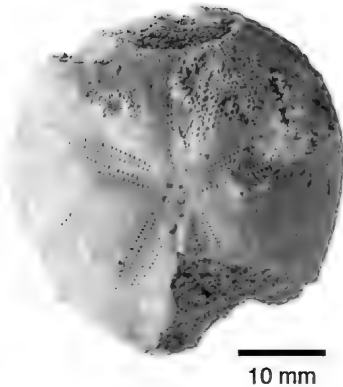


FIGURE 8 Micrasterid indet., WAM 07.431 from the Nanarup lime quarry, W.A., middle Eocene (Bartonian) Nanarup Limestone, aboral view.

**Micrasterid indet.**

## Figure 8

## MATERIAL EXAMINED

**Australia: Western Australia:** WAM 07.431 from the middle Eocene (Bartonian) Nanarup Limestone, Nanarup lime quarry.

## REMARKS

This specimen cannot be assigned to any genus with confidence. Its main characteristics are the possession of four gonopores, an ethmophract apical system, relatively long anterior petals of similar length to the posterior petals, both of which are slightly sunken; it lacks a peripetalous or lateroanal fasciole. It is superficially similar to the Upper Cretaceous to Danian genus *Plesiaster* and also the Paleocene *Pseudogibbaster* and Upper Cretaceous genus *Gibbaster*. Even though it is too incomplete to assign to any of these genera with any degree of certainty, it would seem to be a micrasterid that has lingered deep into the Eocene.

**Family Hemiasteridae H.L. Clark, 1917****Genus *Bolbaster* Pomel, 1869**

## TYPE SPECIES

*Spatangus prunella* Lamarck, 1816, by original designation.

***Bolbaster subidus* McNamara, 1987**

## Figure 9D–F

## MATERIAL EXAMINED

**Australia: Western Australia:** WAM 03.50 and 03.51 from the Nanarup lime quarry, Nanarup Limestone.

## REMARKS

Two relatively well-preserved specimens are both morphologically identical to the type material of the relatively uncommon *Bolbaster subidus* McNamara, 1987 that was described from the contemporaneous Tortachilla Limestone in South Australia. A poorly preserved internal mould of a specimen from the Pallinup Formation in the western Eucla Basin questioningly referred to *Hemiaster* by Martin and McNamara (2004) may also be this species.

**Family Schizasteridae Lambert, 1905****Genus *Schizaster* L. Agassiz, 1836****Subgenus *Paraster* Pomel, 1869**

## TYPE SPECIES

*Schizaster gibberulus* L. Agassiz, 1847, by original designation.

***Schizaster (Paraster) cf. tatei*  
McNamara and Philip 1980b**

MATERIAL EXAMINED

**Australia: Western Australia:** a single, incomplete specimen. WAM 07.430, from the Nanarup lime quarry, Nanarup Limestone.

REMARKS

*Schizaster (Paraster) tatei* McNamara and Philip, 1980b is a relatively common spatangoid in the Bartonian Tortachilla Limestone in South Australia. The only known specimen from the Nanarup Limestone has a large amount of bryozoal and foraminiferal debris adhering to the aboral surface of the test surface making it difficult to ascertain morphological details clearly. The adoral surface is not preserved. The position of the apical system, the lengths and the depths of the petals are reminiscent of the contemporaneous Tortachilla Limestone species and thus it is herein regarded as *S. (Paraster) cf. tatei*. An internal mould of a specimen from the Pallinup Formation has likewise been referred to *S. (Paraster) cf. tatei* (Martin and McNamara 2004).

**Genus *Protenaster* Pomel, 1883**

TYPE SPECIES

*Desoria australis* Gray, 1851b, by original designation.

***Protenaster preaustralis*  
McNamara, 1985a**

Figure 9A–C

MATERIAL EXAMINED

**Australia: Western Australia:** WAM 03.53 from the Nanarup lime quarry, Nanarup Limestone.

REMARKS

This species is the oldest known of the genus. It was described from the Tortachilla Limestone in South Australia on the basis of five specimens (McNamara 1985a). A single specimen is also known from the Wilson Bluff Limestone (McNamara 1985a). The Nanarup Limestone specimen shows slight morphological differences from the previously described material, but this is likely due to ontogenetic differences, as the Nanarup specimen is much smaller than the smallest known topotype specimen, being only 20 mm in length. Topotype material reaches up to 53 mm in length (McNamara 1985a). The anterior notch is particularly faint compared with topotype material (Figure 9A–B), and in this regard is comparable with the living *Protenaster australis* (Gray, 1851b), in which the anterior notch is very faint in juveniles, but deepens significantly during ontogeny (McNamara 1985a). Although very small, the Nanarup specimen of *P. preaustralis* is a young adult, the gonopores being

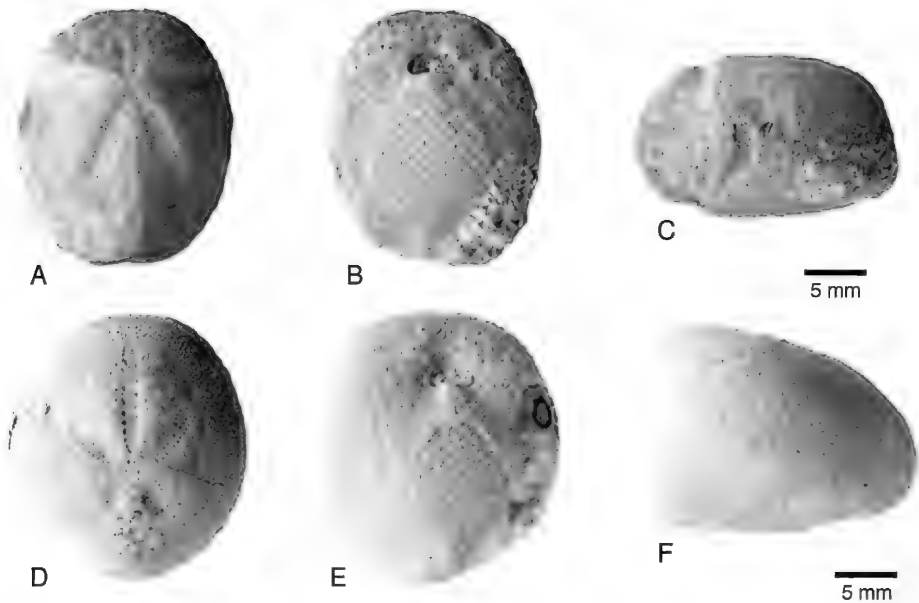


FIGURE 9 *Protenaster preaustralis* McNamara, 1985. A–C, WAM 03.53 from the Nanarup lime quarry, W.A., middle Eocene (Bartonian) Nanarup Limestone: A) aboral; B) adoral; C) left lateral views. *Bolbaster subidus* McNamara, 1987. D–F, WAM 03.51 from Nanarup lime quarry, W.A., middle Eocene (Bartonian) Nanarup Limestone: D) aboral; E) adoral; F) right lateral views.

present. Like the smallest specimen of the living *P. australis* (McNamara 1985a, pl. 32, figs 1–4), the posterior petals are relatively short, being 83% the length of the anterior petals. In the largest specimens of *P. preaustralis* the posterior petals are only slightly smaller than the anterior petals (McNamara 1985a, pl. 33, figs 6–8).

### Family Maretiidae Lambert, 1905

#### REMARKS

Smith and Kroh (2011) suggested that a number of taxa previously included within the Brissidae, and possessing an elongate labral plate and short petals, should not be included within the Brissidae, as genera included within this family typically possess short, wide labral plates. Although they considered that these forms (including *Gillechinus*) could well represent a distinct clade, they prefer to leave them in open nomenclature. Here we consider *Gillechinus* is best placed in the Maretiidae as it possesses reduced pores in anterior ambulacral rows aborally, narrow ambulacra ambitally, relatively elongate wedge-shaped labrum and shield-shaped subanal fasciole.

### Genus *Gillechinus* Fell, 1964

#### TYPE SPECIES

*Gillechinus cudmorei* Fell, 1964, by original designation.

#### *Gillechinus kaitae* sp. nov.

Figure 10

urn:lsid:zoobank.org:act:69BB010A-074D-43D4-BDFB-A8257898A0AC

#### MATERIAL EXAMINED

##### *Holotype*

**Australia: Western Australia:** WAM, 03.13 from the middle Eocene (Bartonian) Manypeaks limestone, Manypeaks lime quarry.

##### *Paratypes*

**Australia: Western Australia:** WAM 07.422a, 07.422b and 07.423 from the same horizon and locality as the holotype; WAM 68.1357 and 07.444 from the middle Eocene (Bartonian) Nanarup Limestone, Nanarup lime quarry.

##### *Other material*

**Australia: Western Australia:** WAM 68.1357, 92.226, 94.824–94.829, 94.830[4], 07.422, 07.423 from the same horizon and locality as the holotype; WAM 07.434[6] from the Nanarup Limestone, Nanarup lime quarry and WAM 76.16 from the Pallinup Siltstone.

#### DIAGNOSIS

Paired petals very shallow and short, about one-quarter test length; posterior slightly longer than anterior. Anterior notch very weak. Aboral interambulacra with few primary tubercles. Peristome relatively long and narrow, with labrum not anteriorly protuberant.

#### DESCRIPTION

Test heart-shaped; up to about 65 mm in length; maximum width varies between 90% and 94% TL at a point roughly 40% from posterior; maximum height varying between 54% and 57% TL, at 35% to 38% TL from posterior. Very weak anterior notch (Figure 10A); posterior of test sharply truncated. Apical system slightly sunken; four gonopores, each ringed by a smooth, raised ridge (Figure 10E). Posterior gonopores tilted and raised to sit above anterior pair. Apical system situated in anterior part of test, at about 35% TL (TL=60.6 mm) and 39% TL (TL=35.5 mm), indicating a shift to anterior with increasing test length. Petals slightly sunken; parallel-sided; open and slightly curved distally; narrow, with very narrow interporiferous zones less than pore pair width; weakly conjugate pores. Posterior petals slightly longer than anterior petals. Anterior petals 26–28% TL; posterior petals 26–32% TL; each with about 20 pore pairs in each row. Ambulacrum III is even less sunken than petals; pore pairs very small, aligned almost exsagittally, with prominent interporal partition. Peripetalous fasciole very thin, thread-like (Figure 11), about 1% TL; not indented between petals; discontinuous across ambulacrum III. Subanal fasciole crescent-shaped, enclosing four or five small pore pairs in ambulacrum I and in ambulacrum V.

Peristome semicircular; wider than long, with length about 60% width; width 13% TL. Periproct lies on truncated posterior surface; almost circular; 13–15% TL. Plastron prominent; triangular, about 30% TL at its widest point above subanal fasciole (28–32% TL). Covered by large tubercles, indicating sediment movement inwards and towards posterior. Labrum broad anteriorly, evenly tapering posteriorly to third adjacent ambulacral plate; 15% TL in length. A keel present extending from behind labrum to posterior, reaching its apex just anterior of subanal fasciole, 58% of distance from posterior of peristome to posterior of test (Figure 10B). Adoral ambulacral zones are extremely wide and featureless, save for a phyllode of single pores, each ambulacrum containing two rows of straight rows of pores.

Aborally, large primary tubercles only occur on posterior series of interambulacral plates and none occur outside peripetalous fasciole. These have bosses that extend well above test surface and aureoles that are not inset and are symmetrical. Numbers vary with size, with the smallest specimen at 35.5 mm TL having about five tubercles in each anterior, and six tubercles in each posterior paired interambulacrum. Largest specimen of about 65 mm TL has no more than 11 tubercles in each interambulacrum. These primary tubercles randomly

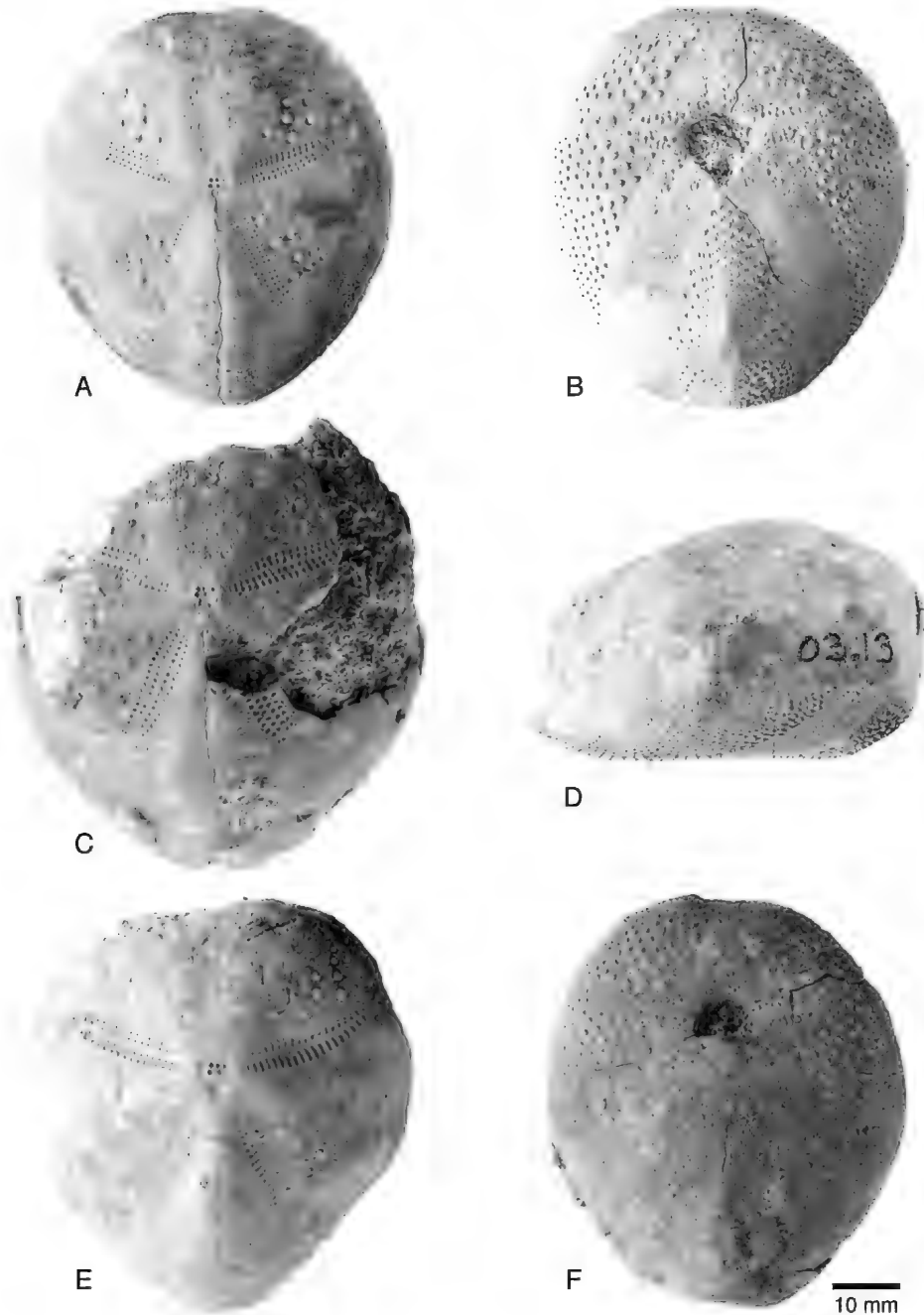


FIGURE 10 *Gillechinus kaitae* sp. nov. A–B, D, holotype WAM 03.13 from the Manypeaks lime quarry, middle Eocene (Bartonian) W.A., Manypeaks limestone: A) aboral; B) adoral; D) left lateral views. C) paratype WAM 07.444 from the Nanarup lime quarry, W.A., middle Eocene (Bartonian) Nanarup Limestone, aboral view. E) paratype WAM 68.1357 from the Nanarup lime quarry, W.A., middle Eocene (Bartonian) Nanarup Limestone, aboral view. F) paratype WAM 07.422a from the Manypeaks lime quarry, W.A., middle Eocene (Bartonian) Manypeaks limestone, adoral view.

arranged on obliquely aligned tubercular surface. Smaller tubercles present along dorsal keel. Adorally, tubercles on interambulacral plates are smaller and more densely arranged, similar in arrangement to the plastron. In all interambulacra, asymmetrical aureoles indicate sediment movement away from peristome — that is, posteriorly and laterally for interambulacra 1 and 4, and anteriorly and laterally for interambulacra 2 and 3.

#### ETYMOLOGY

Named after Kaitie McNamara in recognition of her assistance in helping to collect the Nanarup Limestone echinoids and for collecting many specimens now housed in the Western Australian Museum.

#### REMARKS

The genus *Gillechinus* was erected by Fell (1964) on the basis of material from the Tortachilla Limestone, which he named *G. cudmorei* Fell, 1964. It has been reported from the middle Eocene Tortachilla and Kingscote limestones of the St. Vincent Basin; middle Eocene Wilson Bluff Limestone and late Oligocene-early Miocene Abrakurrie Limestone of the Eucla Basin; and from the late Eocene Pallinup Formation in the western Eucla Basin (McNamara et al. 1986). However, *Gillechinus kaitae*, described herein from the Nanarup and Manypeaks limestones, differs from *G. cudmorei*, in a number of significant ways.

The most notable difference is the possession of fewer aboral primary interambulacral tubercles in the new species. Small specimens (between 35 and 45 mm in test length) of both species from the Tortachilla, Nanarup and Manypeaks limestones all have a similar number of tubercles (between 1 and 7) in each interambulacrum. However, whereas large specimens (about 60 mm test length) of *G. cudmorei* from the Tortachilla Limestone have up to 36 tubercles (McNamara et al. 1986, fig. 11C), comparable-sized specimens of *G. kaitae* from the Nanarup Limestone have less than a third of this, with a maximum known 11. The Pallinup Formation *Gillechinus* species originally assigned to *G. cudmorei* is herein also considered to be *G. kaitae*.

*Gillechinus kaitae* can further be distinguished from *G. cudmorei* by its shallower paired petals, which are also significantly shorter, the anterior pair being 26–28% TL in the former species compared with 36–38% TL in the latter. Similarly, the posterior petals are significantly shorter in *G. kaitae*, 28–32% TL, compared with 34–35% TL. Ambulacrum III is extremely shallow in *G. kaitae*, as is the anterior notch, unlike *G. cudmorei*. Moreover, the peristome is longer and narrower, as the labrum does not project anteriorly. The apex of the plastral keel is also located more anteriorly in *G. kaitae*.

A specimen figured by Smith and Kroh (2011) from the Wilson Bluff Limestone in the eastern Eucla Basin (Museum of Victoria specimen PI49924) and called by them *G. cudmorei*, has all the attributes of *G. kaitae*, to which species it should be assigned. This demonstrates that this species was relatively widely distributed across the Eucla Basin during the Bartonian Tortachilla Transgression.

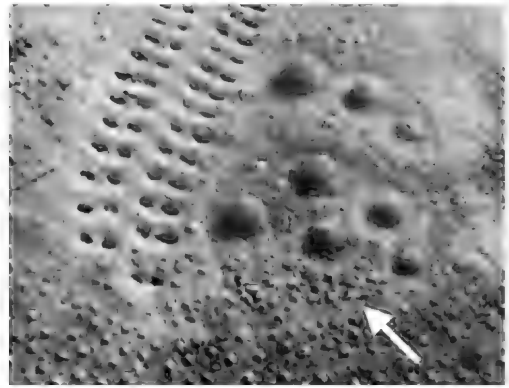


FIGURE 11 *Gillechinus kaitae* sp. nov., WAM 03.13, holotype, from the Manypeaks lime quarry, middle Eocene (Bartonian) W.A., Manypeaks limestone; oblique posterolateral aboral closeup, showing thin peripetalous fasciole (arrowed) skirting interambulacrum 4 and ambulacrum V.

*Gillechinus kaitae* can be distinguished from *G. sindensis* (Duncan and Sladen, 1884) from the Eocene of the Sind region of Pakistan by its broader test, shallower petals, ambulacrum III and anterior notch and more centrally located apical system. *G. alabamensis* (Cooke, 1942) from the Eocene of the south-eastern USA has even fewer aboral primary interambulacral tubercles, deeper, longer petals and more prominent labrum.

## EUCLA BASIN MIDDLE-LATE EOCENE ECHINOID BIOFACIES

### NANARUP AND MANYPEAKS LIMESTONES

In terms of numbers of specimens, the echinoid fauna of the Nanarup Limestone is dominated by *Echinolampas*, *Fossulaster* and *Temnocidaris* (*Stereocidaris*) (Table 1). The cassiduloid *Echinolampas* is overwhelmingly dominant, comprising almost 70% of the specimens recovered (excluding cidaroids, because of their invariably incomplete preservation). The next most abundant taxon, *Fossulaster*, comprises 17% of the specimens collected. Other taxa comprise less than 10% each (Table 2). In contrast, the Manypeaks limestone is dominated by the spatangoid *Gillechinus*, with *Fossulaster* comprising 20% of the specimens collected (n=40).

The transition from the coarser Nanarup grainstone biofacies to the more silty Manypeaks biofacies probably represents a bathymetric transition from shallower, middle shelf facies to deeper water, outer shelf facies (Boreen and James 1995). The most notable change in the biofacies is the transition from a cassiduloid/clypeasteroid-dominated Nanarup biofacies to a spatangoid-dominated Manypeaks biofacies.



The percentage of the cassiduloid *Echinolampas* in the assemblages differs markedly, from 69% in the Nanarup biofacies to 12% in the Manypeak biofacies, while the spatangoid *Gillechinus* represents just 5% of the Nanarup biofacies, compared with 47.5% of the Manypeaks biofacies (Table 2). However, despite the increase in overall spatangoid numerical diversity in the Manypeaks biofacies, species diversity is different. *Protenaster*, *?Isaster* and *Bolbaster*, although rare elements in the Nanarup biofacies, are not present

in the Manypeaks limestone; while *Gillechinus*, *Cyclaster*, *Eurhodia*, *Pleurosalenia*, *Ortholophus* and *Australanthus* become relatively a little more common.

McNamara (1993) recorded a similar pattern in late Oligocene limestones in the Torquay Basin. Here the coarse bryozoal grainstones of the Point Addis Limestone are dominated by cassiduloids and clypeasteroids. The finer-grained Waurrn Ponds Limestone, however, is dominated by spatangoids (about 70% of species and specimens). The cassiduloid/

TABLE 1 Numbers of specimens of middle Eocene echinoids from the Nanarup Limestone and Manypeaks limestone, western Eucla Basin, W.A., including the nature of preservation, where 'whole' specimens are those with more than half the test preserved, 'partial' specimens preserve around half the test, and 'fragments' preserve less than half the test surface.

A) Nanarup Limestone species	Specimens	Whole	Partial	Fragments
<i>Temnocidaris (Stereocidaris) cudmorei</i>	72	0	72	??
<i>Ortholophus</i> aff. <i>bittneri</i>	14	4	10	0
<i>Pleurosalenia tertiaria</i>	1	1	0	0
<i>Echinolampas posterocrassa</i>	380	37	343	0
<i>Australanthus longianus</i>	22	1	17	4
<i>Eurhodia westaustraliae</i>	3	0	3	0
<i>Fossulaster susae</i>	96	39	53	4
<i>?Isaster</i> sp.	1	0	1	0
<i>Protenaster preaustralis</i>	1	1	0	0
<i>Schizaster (Paraster) cf. tatei</i>	1	1	0	0
<i>Bolbaster subidus</i>	2	1	1	0
<i>Gillechinus kaitae</i>	28	0	14	14
<i>Cyclaster jamiei</i>	3	0	3	0
Micrasterid indet.	1	0	1	0
<b>Total (excluding cidaroid spines)</b>	<b>627</b>	<b>86</b>	<b>519</b>	<b>22</b>
B) Manypeaks limestone species	Specimens	Whole	Partial	Fragments
<i>Temnocidaris (Stereocidaris) cudmorei</i>	2	0	2	0
<i>Ortholophus</i> aff. <i>bittneri</i>	2	0	0	2
<i>Pleurosalenia tertiaria</i>	1	1	0	0
<i>Echinolampas posterocrassa</i>	5	2	3	0
<i>Australanthus longianus</i>	3	0	1	2
<i>Eurhodia westaustraliae</i>	1	1	0	0
<i>Fossulaster susae</i>	8	4	4	0
<i>Cyclaster jamiei</i>	1	0	1	0
<i>Gillechinus kaitae</i>	19	4	8	7
<b>Total (excluding cidaroid spines)</b>	<b>42</b>	<b>12</b>	<b>19</b>	<b>11</b>

clypeasteroid and spatangoid biofacies form a dominance continuum, paralleling the transition from coarser to finer-grained sediments in shelf transects from the higher hydrodynamic energy of the inner mid-shelf, to the quieter, deeper waters of the outer-shelf. This environmental continuum is reflected in the biofacies seen in the western Eucla Basin. While the Nanarup Limestone represents a near 'complete' cassiduloid/clypeasteroid biofacies (more than 90% of specimens), the Manypeaks marly limestone is more transitional to a 'complete' spatangoid biofacies in that spatangoids comprise 50% of the Manypeaks specimens, the cassiduloids/clypeasteroids just over 40%. A 'complete' spatangoid biofacies is only seen in Cenozoic sediments in southern Australia in the middle Miocene Rutledge Marl, where spatangoids comprise 100% of the echinoid fauna (McNamara 1991) in these muddy sediments. A comparable pattern of cassiduloid/clypeasteroid and spatangoid biofacies has been documented by Challis (1979) in the Miocene of Malta.

The absence of the spatangoids *Protenaster*, *Bolbaster* and *?Isaster* from the finer-grained Manypeaks limestone indicates that during the middle Eocene these genera were still adapted to inhabiting a relatively coarse, permeable substrate and had yet to evolve the morphologies to cope with burrowing in fine-grained sediments, despite later species being tolerant of such

sediments (McNamara 1985a, 1987). However, the greater proportion of *Gillechinus* in the Manypeaks limestone indicates that this form was already adapted to inhabiting fine-grained sediments and indeed preferred them to sandier substrates. In the case of *Protenaster* (McNamara 1985a) and *Bolbaster* (McNamara 1987) previous assessments of the genera similarly identified these middle Eocene species as sand-tolerant, with later forms becoming gradually adapted to finer substrates. As the changes in the proportions of other cassiduloid and clypeasteroid species are only small, it is assumed that these changes are not real increases or decreases, but are caused by the large change in the amount of *Echinolampas posterocrassa* in the assemblage.

Using biological population statistics, the diversity and dominance of the echinoid assemblages can be assessed. For individual faunas, the species diversity can be calculated using Simpson's  $\alpha$  diversity index  $D = 1 - \sum(n_i/N)^2$ , where  $D$  is the diversity of the population,  $n_i$  is the number of individuals in a species and  $N$  is the total number of individuals in the population. Thus, if  $D = 0$ , there is no diversity, with only one species present (high dominance); while  $D = 1$  represents equal amounts of individuals in each species present (low dominance; Knox et al. 2001). Omitting the regular echinoid *Temnocidaris* (*Stereocidaris*) due to the indeterminate numbers of individuals represented, the

TABLE 2 Proportions of species preserved in the Nanarup Limestone and Manypeaks limestone. *Temnocidaris* (*Stereocidaris*) *cutmorei* is not included because the fragmented nature of these specimens does not allow accurate estimation of the population size.

Species	% of Nanarup	% of Manypeaks
<i>Australanthus longianus</i>	4.0	7.5
<i>Cyclaster jamiei</i>	0.5	2.5
<i>Echinolampas posterocrassa</i>	69.0	12.5
<i>Eurhodia westaustraliae</i>	0.5	2.5
<i>Fossulaster susae</i>	17.4	20.0
<i>Gillechinus kaitae</i>	5.1	47.5
<i>Bolbaster subidus</i>	0.4	-
<i>Ortholophus</i> aff. <i>bitneri</i>	2.5	5.0
<i>?Isaster</i> sp.	0.2	-
<i>Protenaster preaustralis</i>	0.2	-
<i>Pleurosalenia tertiaria</i>	0.2	2.5
<b>Total</b>	<b>100.0 (n=551)</b>	<b>100.0 (n=40)</b>

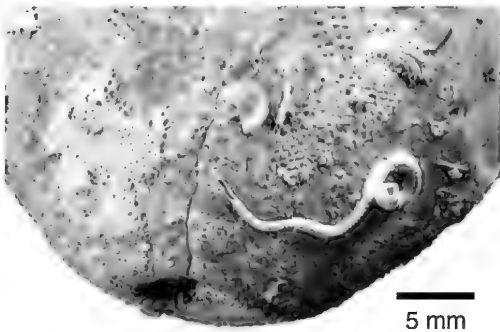


FIGURE 12 Bryozoal and serpulid epibionts on posterior part of aboral surface of a specimen of *Gillechinus kaitae* sp. nov., WAM 07.423, from the Manypeaks lime quarry, W.A., middle Eocene (Bartonian) Manypeaks limestone.

Nanarup Limestone has an  $\alpha$ -diversity  $D$  of 0.489, with a species richness of 11. In the Manypeaks limestone  $D = 0.697$  and species richness is 8. Thus, while the Nanarup Limestone has a larger number of species, the dominance of the assemblage is high; and although the Manypeaks limestone may have lower dominance, there are fewer species.

Low alpha-diversities, representing high dominance assemblages, are generally considered indicators of environmental disturbance, the cause of which may be external (environmental) or internal (biological). In the case of the Nanarup Limestone, *Echinolampas posteroocrassa* appears to have been an opportunistic species, able to deal with conditions better than other species, allowing it to thrive. In the Manypeaks environment, this disturbance was reduced, leading to lower dominance and higher alpha-diversity, suggesting that water depth or substrate were the cause. It has been noted that dominance tends to increase in shallow-water communities due to energy and exposure pressures, but this trend is generally accompanied by lower species richness (Dodd and Stanton 1981), which is not seen in the Nanarup Limestone.

Evidence for instability and sediment disturbance, particularly in the Nanarup Limestone, is provided by the frequency of occurrence of epibionts on the irregular echinoids. Discounting very small, poorly preserved or worn specimens, about two-thirds of specimens from both limestones have some degree of encrustation by epibionts (e.g., Figure 12). The principal epibionts are bryozoans, with a few being serpulids. Boren and James (1995) have pointed out that many of the bryozoal grainstones of the southern Australian Cenozoic sediments were deposited above storm wave-base. Post-mortem exhumation of the echinoids must have been

common, as shown by the frequent presence of epibionts on both the aboral and adoral surfaces. The period of exhumation was probably not that long. Nebelsick et al. (1997) have observed how dead tests of modern species of *Schizaster* can become completely encrusted by epibionts within about a year. While many of the Nanarup specimens are epibiont encrusted, the bryozoal colonies are relatively small (less than 1 cm in diameter), suggesting perhaps short periods of exhumation before being re-covered in the next storm event.

Some specimens from the Manypeaks limestone are heavily iron-stained (e.g. see Figure 4D–F), again indicating reasonably long exposure on the sea floor during periods of little to no sedimentation in the deeper water environment. Some taxa in the Nanarup Limestone, notably *Bolbaster* and *Protenaster*, do not show any evidence of encrustation by epibionts. This could suggest that, as deeper burrowers, they were less prone to post-mortem exhumation, but sample numbers are too small to demonstrate this conclusively.

#### *Marsupiate Echinoids*

One interesting aspect of both the Nanarup and Manypeaks limestones is the marsupiate echinoid *Fossilaster susae* described herein. This species is the oldest known marsupiate echinoid in the Australian Cenozoic. Marsupiate echinoids are unknown in the contemporaneous Tortachilla Limestone. This first marsupiate occurrence in the western end of the southern Australian margin during the middle Eocene, with a later occurrence of such echinoids in the east during the late Eocene, reinforces the notion of a progressive easterly spread of marsupiates during the Cenozoic, reflecting the overall, general migration pattern seen in echinoids (Foster and Philip 1978; McNamara 1999).

Although a number of studies have suggested that the occurrence of such brooding echinoids was indicative of cool water conditions (Rowe and Vail 1982; Smith 1984; Néraudeau et al. 2003; Dudicourt et al. 2005), due to their modern ubiquity in high latitude polar waters, McNamara (1994a) has argued that there is no correlation between diversity of marsupiate echinoids in the Cenozoic rock record in southern Australia and palaeotemperatures. Rather, he suggested, as have others (Clarke 1988; Poulin and Féral 1995), that the biodiversity of brooding in echinoids is greatly influenced by environmental seasonality. In the modern environment, marsupiate echinoids are most common in polar regions where the shortened period of sunlight means a short period of phytoplankton bloom, and thus a shortened period for feeding — stressed, but predictable. These conditions favour forms that can coordinate reproduction with these high nutrient conditions, produce small numbers of offspring, and invest considerable energy into reproduction, features which are characteristic of brooding echinoid reproduction (Jeffery and Emler 2003). Thus, the presence of the marsupiate echinoid *Fossilaster susae* within the middle

Eocene limestones of the western Eucla Basin, suggests a degree of seasonality in the environment of this area during this time. This is supported by arguments that the development of extensive terrestrial silcretes and seasonally adapted vegetation at this time nearby were due to high seasonality (Carpenter et al. 2014).

#### PALLINUP FORMATION

The Nanarup Limestone is overlain by the clastic and lignitic Werillup Formation (Cockbain 1968; Clarke et al. 2003). This in turn is overlain by the siliceous Pallinup Formation, the upper Fitzgerald Member of which is a fossiliferous spongolite. These rocks extend for about 1000 km, from near Albany in the west, close to Israelite Bay in the east (Gammon and James 2001, fig. 2). The Pallinup Formation contains an echinoid fauna that is essentially undescribed at the species level. The calcareous biota has been leached away and specimens are preserved as internal and external moulds. The unit has been correlated with late Eocene planktonic foraminiferal zones P15 and P16, and represents part of the Tuketja Transgression across southern Australia (Clarke et al. 2003; Hou et al. 2008). The only echinoids previously reported from the Pallinup Formation are the spatangoids *Linthia pulchra* (McNamara 1985b), *Gillechinus kaitae* (as *G. cudmorei* (McNamara et al. 1986)) and a single specimen of the cassiduloid *Aphanophora? bassoris* Holmes, 1995 (Martin and McNamara 2004). The echinoid fauna of the Pallinup Formation, as represented by specimens in the Western Australian Museum (McNamara pers. obs.), is a spatangoid biofacies, being dominated by spatangoids including, in addition to *L. pulchra* and *G. kaitae*, *Bolbaster* sp., *Schizaster* (*Paraster*) *tatei*, *Isaster* sp., *Cyclaster jamiei* and *Pericosmus* sp. The only non-spatangoids, apart from *Aphanophora?* are the holasteroid *Giraliaster bellissae* Foster and Philip, 1978 and the cidaroid *Temnocidaris* (*Stereocidaris*) sp.

Whereas the Nanarup Limestone contains a cassiduloid/clypeasteroid, shallow burrowing biofacies and the Manypeaks limestone a mixed spatangoid/cassiduloid biofacies, the Pallinup Formation is dominated by a spatangoid biofacies, containing both shallow and deeper burrowing forms. The Pallinup Formation has been identified as having been deposited in a shallow-water, warm-temperate humid environment (Gammon and James 2003) as opposed to the deep, cool-water environment it was originally considered to be (Gammon et al. 2000, Gammon and James 2001), suggesting that the echinoid faunas of the southern Australian margin may have been strongly influenced by sediment grain size and not just water depth and temperature.

#### TORTACHILLA LIMESTONE

The Tortachilla Limestone is the South Australian equivalent of the Nanarup Limestone and contains a rich echinoid fauna, comprising cidaroids (*Temnocidaris* (*Stereocidaris*) *cudmorei*, *T. (Stereocidaris) fosteri*,

*T. (Stereocidaris) inermis*, *T. (Stereocidaris) hispida*, *T. (Stereocidaris) intricata*), saleniids (*Pleurosalenia tertiaria*), temnopleurids (*Ortholophus bittneri*, *Tatechinus nudus*), clypeasteroid (*Fibularia gregata*), cassiduloids (*Apatapygus vincentinus*, *Australanthus longianus*, *Eurhodia australiae*), echinolampadoid (*Echinolampas posteroocrassa*), holasteroids (*Giraliaster bellissae*, *G. sulcatus*, *G. tertiarius*), neolampadids (*Pisolampas concinna*, *Aphanopora? bassoris*) and spatangoids (*Gillechinus cudmorei*, *Bolbaster subidus*, *Linthia pulchra*, *Prenaster aldingensis*, *Protenaster preaustralis*, *Psephoaster lissos* and *Schizaster* (*Paraster*) *tatei*) (Holmes, 1999). Many of the elements present in the Pallinup Formation and in the Nanarup and Manypeaks limestones also occur in the Tortachilla fauna (Table 3).

This Tortachilla assemblage is noticeably richer taxonomically than the western Eucla units. This is unlikely to be a factor of greater collecting of the Tortachilla Limestone, because both the Tortachilla and Nanarup limestones have been extensively collected over many years. This higher species richness at Tortachilla could be related to greater variability in substrate, which has been noted to vary between sandy and marly (Lindsay 1969). Alternatively, if the disturbance that appears to cause the high dominance in the Nanarup Limestone was absent in the Tortachilla Limestone, one would expect this higher species richness, coupled with lower dominance. The fact that there is no evidence for gastropod predation in the Tortachilla Limestone during the middle Eocene (McNamara 1994b) supports the theory that predation pressure was the cause for this disturbance in the Nanarup Limestone, where there is evidence for gastropod predation (e.g. see Figure 3C). For instance, of the 380 specimens of *Echinolampas posteroocrassa* collected from the Nanarup Limestone 11%, show evidence of gastropod predation. Interestingly, the middle Eocene marks the time when there was a distinct increase in echinoid predation globally, corresponding to an increase in diversity of cassid gastropods, one of their most common predators (Petsios et al. 2021).

Comparison of the western Eucla and the St Vincent basin assemblages can be undertaken using Jaccard's  $\beta$  diversity constant,  $S = a/t$ , where  $S$  is Jaccard's constant of genus comparison in two areas,  $a$  = number of shared genera, and  $t$  = total number of genera. Thus, if  $S = 0$ , the assemblages in the two areas are completely different and share no genera. If  $S = 1$ , the assemblages are exactly the same and the areas have identical populations (Knox 2001). For Nanarup and Manypeaks  $S = 0.75$ , while for Pallinup and Manypeaks  $S = 0.13$ , and comparing Nanarup and Pallinup,  $S = 0.24$ . These calculations confirm the close comparison between the Manypeaks and Nanarup limestones, and also confirm the lack of similarity between the Nanarup Limestone and Pallinup Formation assemblages. Although the Pallinup fauna seems most like that of the Nanarup Limestone, this may be due to the greater

TABLE 3 Presence and absence of genera from middle and late Eocene units of southern Australia, with a '–' indicating a genus' absence, and a '+' the genus' presence in a unit. Tortachilla assemblage information from Holmes (1999, Appendix 1).

Genus	Nanarup Limestone	Manypeaks limestone	Pallinup Formation	Tortachilla Limestone
<i>Apatopygus</i>	–	–	+	+
<i>Aphanopora?</i>	–	–	+	+
<i>Australanthus</i>	+	+	–	+
<i>Bolbaster</i>	+	+	+	+
<i>Cyclaster</i>	+	+	+	0
<i>Echinolampas</i>	+	+	–	+
<i>Eurhodia</i>	+	+	–	+
<i>Fibularia</i>	–	–	–	+
<i>Fossilaster</i>	+	+	–	–
<i>Gillechinus</i>	+	+	+	+
<i>Giraliaster</i>	–	–	+	+
<i>?Isaster</i>	+	–	–	–
<i>Linthia</i>	–	–	+	+
<i>Micrasterid</i> indet.	+	–	–	–
<i>Ortholophus</i>	+	+	–	+
<i>Pericosmus</i>	–	–	+	–
<i>Pisolampas</i>	–	–	–	+
<i>Prenaster</i>	–	–	+	+
<i>Protenaster</i>	+	–	–	+
<i>Psephoaster</i>	–	–	–	+
<i>Pleurosalenia</i>	+	+	–	+
<i>Schizaster (Paraster)</i>	+	–	+	+
<i>Temnocidaris (Stereocidaris)</i>	+	+	+	+
<i>Tatechinus</i>	–	–	–	+

number of specimens and species at Nanarup than at Manypeaks. As noted, the slight difference between the faunas of Nanarup and Manypeaks appears to be due to a slight difference in sediment type, which in turn may be due to variation in water depth.

When comparing Western Australian and South Australian assemblages, Nanarup and Tortachilla have  $S = 0.48$ , for Manypeaks and Tortachilla  $S = 0.33$ , and for Pallinup and Tortachilla  $S = 0.4$ . Thus neither Nanarup nor Manypeaks is distinctly more like the Tortachilla fauna. As the Tortachilla Limestone has species similar to both the coarse-grained (Nanarup) and fine-grained (Pallinup) units, it appears to contain both these substrates. Therefore, if all three western Eucla units are compared with the Tortachilla Limestone  $S = 0.64$ , they are not entirely dissimilar. There are seven genera

that are not shared between Western and South Australia — *Cyclaster*, *Fossilaster* and *Pericosmus* occur only in the western Eucla Basin, while *Pisolampas*, *Tatechinus*, *Psephoaster* and *Fibularia* only occur in the Tortachilla Limestone. It is possible that if the deepest water phase of the Nanarup environment was preserved, those forms missing in the Eucla Basin, but found in the Tortachilla Limestone, would be present.

As a number of genera and species are shared between the Eucla and St. Vincent basins during the middle-late Eocene, it appears there was good connectivity between southern Australian echinoid faunas during this period. McNamara (1999) previously noted the similarities between the Nanarup Limestone assemblage and that of the contemporary Giralia Calcarenite of the Southern Carnarvon Basin, revealing that this connectivity

extends both down the western and across the southern coast. This he attributed to the action of the proto-Leeuwin Current, activated by the warm climate during the middle and late Eocene. In recent times, the Leeuwin Current is well known for bringing invertebrate larvae from the tropical northwest to higher latitudes, along with warmer water in the process. The current flow would also have encouraged the migration of echinoid species from the Eucla Basin to the St Vincent Basin, enhancing the similarity in faunas.

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# Notes on a new method to identify Golden Bandicoot and Northern Brown Bandicoot in the Kimberley region

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**ABSTRACT** – The two species of bandicoots that occur in the Kimberley region are particularly difficult to tell apart as they have no distinctive features other than size. A new method is proposed here to identify the two species based on dental measurements, by taking an imprint of the teeth with dental impression paste. The new technique can accurately reproduce the size of the teeth and help identify the species quickly and cheaply. This method still needs to be tested on live specimens but provides an alternative to species identification using DNA analysis.

**KEYWORDS:** Dental imprint, *Isoodon*, species identification

## INTRODUCTION

The Kimberley region in Western Australia is the home of two species of bandicoots, the smaller Golden Bandicoot, *Isoodon auratus* (Ramsay 1887), and the larger Northern Brown Bandicoot, *Isoodon macrourus macrourus* (Gould 1842; Van Dyck and Strahan 2008). While the name of each species suggest that they can be identified using pelage colour, this is not the case, as both are brown in overall colour, which renders the identification of individual specimens quite difficult, with overall size the only way to tell them apart in the field. However, size is problematic as a young Northern Brown Bandicoot can be the same size as an adult Golden Bandicoot. A genetic sample can be used to verify the identification, but this is a costly method and takes time before the results are known. A cheaper and faster method would be therefore welcomed to identify the two species in the field (S. Cameron pers. comm.). Considering that the two species are easily identifiable using dental and cranial morphology (Warburton and Travouillon 2016), a new method is proposed here using dental impression paste as a way to identify the two species.

## METHODS

The new method was tested on a recently deceased Golden Bandicoot specimen (WAM M65293), collected from Mitchell Falls, Mitchell Plateau, Kimberley. The specimen was thawed a day prior to make sure its mouth could be easily opened. SS White Impression paste was used to take the dental impression. The white-zinc

oxide paste was mixed in equal amount with the red-eugenol paste to form a single pink paste (Figure 1A). The directions for use suggest that it can be used after 30 seconds of mixing, up to 2 minutes 45 seconds. When the paste was applied to the teeth during that working window, the paste was too sticky and was hard to remove from the teeth. During a second attempt, at least 3 minutes passed before it was applied, making sure it was dry to the touch, with a plastic stick (Figure 1B), used to press the paste onto the upper molars to obtain an imprint. The second attempt was successful, and a clean imprint was recovered very quickly by pressing gently on the upper molars (Figure 1C–D). It took less than 5 seconds to open the mouth and obtain the imprint before closing the mouth again.

The imprint was photographed and measured using a Leica microscope M205 A, with a Leica camera DMC4500. Measurements of the molars were then compared to measurements taken on museum specimens, using callipers, for both the Kimberley Golden Bandicoot (*Isoodon auratus*) and the Northern Brown Bandicoot (*Isoodon macrourus macrourus*). All specimens of the Kimberley Golden Bandicoot are from the Western Australian Museum (Perth). Specimens of the Northern Brown Bandicoot are from the Western Australian Museum (Perth), Natural History Museum (London, UK), Queensland Museum (Brisbane), Australian National Wildlife Collection (Canberra), Museum and Art Gallery of the Northern Territory (Darwin) and the Australian Museum (Sydney). The measurements were summarised as univariate statistics, analysed in the software PAST (Hammer et al. 2001).

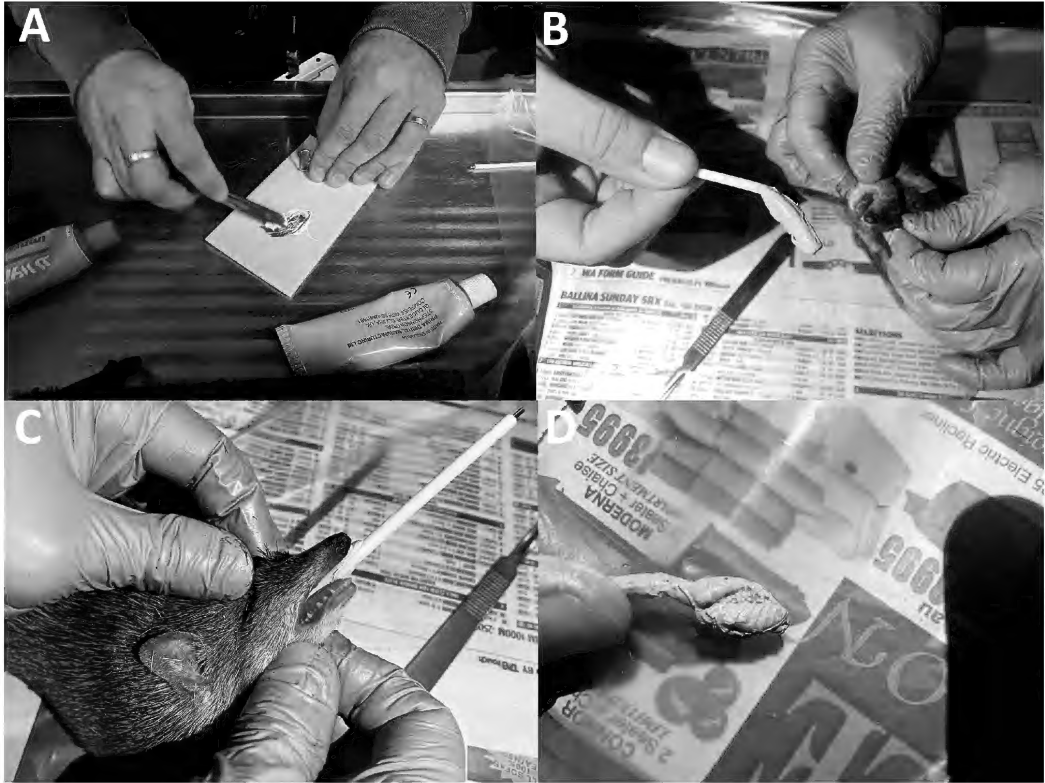


FIGURE 1 Photos showing each step of the dental paste method.

## RESULTS

The imprint successfully reproduced the shape and size of the M1, M2 and a partial M3 (Figure 2A). The measurements were taken digitally on the photograph taken with the Leica microscope, but callipers could have been equally successful. When compared with the actual teeth measurements, after the specimen was prepared (Figure 2B), the measurements are very close for the lengths of M1–3, but the width is much less accurate, and is overestimated in the dental imprint.

Univariate statistics for the dental measurements for the two species of bandicoots are shown in Table 1. Measurements of the M4 and m4 are not provided here, as it is unlikely that an imprint of these teeth can be done easily as they are further back in the mouth. All measurements taken on the imprint fall within the range of the Golden bandicoot.

## DISCUSSION

The new method presented here successfully recovered an accurate imprint of the teeth of the animal, allowing them to be measured to identify the species.

There is little overlap in the dental measurements of the two species (Table 1), which makes this method very easy to use. It should be useable in the field, only taking minutes to prepare the impression paste, so it can be applied very quickly, and get a result soon afterwards. The lengths of the teeth imprints are the most accurate representation of teeth measurements and should be used primarily. Despite the difference in measurements for the widths between the imprints and the teeth, the imprint measurements are still within the range expected for the Golden Bandicoot, and therefore can still be used for the identification.

This method has only been tested on a single recently dead specimen and should be tested on living specimens before it can be widely used, but ethics approval will be required to test this method in the field. The biggest challenge is not the method itself, but getting the animal to open and close its mouth without causing too much stress to the animal. However, a tickle under the chin seems to trigger the mouth of bandicoots to open widely (S. Cameron, pers. comm.). If this is correct, this means that it should be relatively easy to do this method.

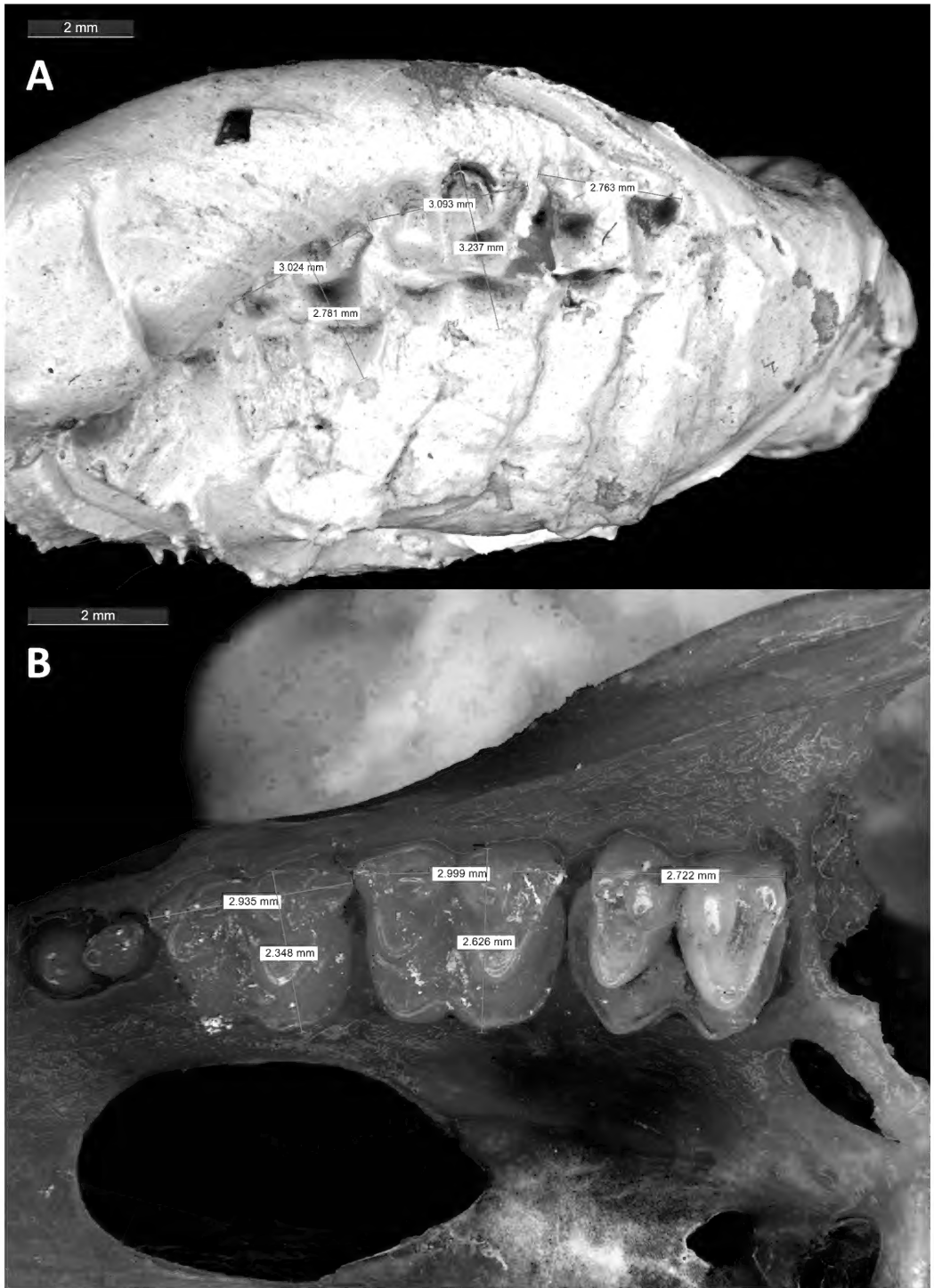


FIGURE 2 Golden Bandicoot, *Isoodon auratus* (WAM M65293). A) dental imprint of the left M1-3, with measurements; B) left M1-3 with measurements.

TABLE 1 Univariate statistics of dental measurements of the upper (M1-M3) and lower molars (m1-3).  
L = length, AWW = anterior width, PW = posterior width, W = width.

	M1L	M1W	M2L	M2W	M3L	M3W	m1L	m1AW	m1PW	m2L	m2AW	m2PW	m3L	m3AW	m3PW
<i>Isoodon auratus</i> (Kimberley population)															
Sample size (N)	34	34	34	34	32	32	36	36	36	36	36	36	36	36	36
Minimum size	2.72	2.42	2.62	2.69	2.35	2.08	2.45	1.48	1.79	2.61	1.91	2.16	2.70	2.01	2.11
Maximum size	3.30	3.00	3.43	3.36	3.34	3.60	3.14	1.91	2.34	3.37	2.34	2.74	3.33	2.35	2.65
Mean	3.03	2.72	2.95	2.97	2.82	3.18	2.76	1.70	2.08	3.02	2.08	2.43	3.05	2.16	2.33
<i>Isoodon macrourus macrourus</i>															
Sample size (N)	120	120	129	129	126	126	125	125	125	126	126	126	122	122	122
Minimum size	3.21	2.99	3.36	3.20	3.56	3.43	2.93	1.96	2.31	3.16	2.27	2.74	3.06	2.30	2.53
Maximum size	4.45	4.12	4.28	4.84	4.65	5.03	4.20	2.86	3.20	4.59	3.46	4.07	4.78	3.30	4.02
Mean	3.82	3.56	3.78	3.99	4.07	4.19	3.43	2.28	2.72	3.79	2.78	3.17	4.00	2.95	3.07

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